THE AMPHIPOD SUPERFAMILY COROPHIOIDEA ON THE PACIFIC COAST OF NORTH AMERICA. PART V. FAMILY COROPHIIDAE: COROPHIINAE, NEW SUBFAMILY. SYSTEMATICS AND DISTRIBUTIONAL ECOLOGY.

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ABSTRACT

Based on extensive new material from North American Pacific coastal marine waters, and on the previous literature, the nominate subfamily, Corophiinae, is newly proposed within family Corophiidae Dana, 1849, to encompass the polymorphic genus *Corophium* Latreille, 1806 sens. lat. World-wide, the new subfamily embraces 13 genera world-wide of which 6 relatively primitive genera have unfused urosomal segments and member species are primarily free-burrowing in soft sediments, and 7 relatively advanced genera that have fused urosomal segments and component species typically construct open-ended tubes on hard substrata. The following 10 genera are represented in the North Pacific region: ***Eocorophium***, new genus [Type species - *E. kitamori* (Nagata, 1965)]; ***Sinocorophium***, new genus [Type species- *S. sinensis* (Zhang, 1974)]; ***Americorophium***, new genus [Type species - *A. spinicorne* (Stimpson, 1857)]; ***Microcorophium***, new genus [Type species- *M. miospinulosum* (Hirayama, 1986)]; ***Lobatocorophium***, new genus (Type species - *L. lobatum* (Hirayama, 1987)]; ***Crassicorophium***, new genus (Type species - *C. crassicornis* (Bruzelius, 1859)]; ***Hirayamaia***, new genus [Type species - *H. mortoni* (Hirayama, 1986)]; ***Monocorophium***, new genus [Type species - *M. insidiosum* (Crawford, 1937)]; ***Apocorophium***, new genus [Type species - *A. acutum* (Chevreux, 1908)]; and ***Laticorophium***, new genus [Type species - *L. baconi* (Shoemaker, 1934a)]. The following 3 genera are restricted variously to the northeastern North Atlantic, Mediterranean and Aralo-Caspian regions: *Corophium* Latreille, 1908 [Type species - *C. volutator* (Pallas, 1776)]; ***Medicorophium***, new genus [Type species - *M. aculeatum* (Chevreux, 1908)], and ***Chelicorophium***, new genus [Type species- *C. chelicorne* Sars, 1895b)].

In the present study of the subfamily in coastal marine and brackish waters, from Alaska to northern California, the following species are recorded, redescribed, variously refigured, and keyed. *Americorophium spinicorne* (Stimp.), *A. salmonis* (Stimp.), *A. stimpsoni* (Shoem.), *A. brevis* (Shoem.), *Crassicorophium crassicorne* (Bruz.), *Monocorophium insidiosum* (Crawf.), *M. steinegeri* (Gurj.), *M. acherusicum* (Costa), *M. californianum* (Shoem.), and *Laticorophium baconi* (Shoem.). Newly described within *Monocorophium* and recorded here is ***M. carlottensis***, new species. Five other regionally peripheral species, *Crassi-corophium* clarencense (Shoem.) and C. *bonelli* (M.-E.), arctic and subarctic shallow-water species, *Monocorophium oaklandense* (Shoem.), a cool water Californian endemic, and *M. uenoi* (Nagata) and *Sinocorophium alienense* (Chapman), synanthropic in San Fancisco Bay, are also redescribed, figured and keyed.

Taxonomically, previously employed character states such as the degree of fusion of the urosomal segments, form of the mandibular palp, and degree of ventral insertion of uropods were found to exhibit homoplasious similarity in otherwise distantly related genera, and thus appear unreliable as a basis for cladistic classification within the subfamily. Phyletically, the endemic North American Pacific corophiin fauna exhibits strong affinities to that of the western North Atlantic, but little to that of the eastern North Atlantic and Mediterranean regions, and apparently none to the Asiatic North Pacific fauna. Of the warm-temperate species of *Monocorophium* from central and southern California, only *Corophium californianum* ranges northward to British Columbia. The three species of *Crassicorophium* occurring in northern parts of the study region are arctic-subarctic in biogeographic affinities and may be closest phyletically to the primitive, mainly sublittoral Mediterranean endemic genus *Medicorophium.* We may conclude that the Corophiinae are relatively recently evolved, and have two main centres of origin and dispersal, viz., primarily in the western North Pacific, from whence they have apparently radiated, post-Tethyan, to the North Atlantic, and secondarily in the North Pacific region wherein most advanced generic types have recently radiated.

INTRODUCTION

Studies on North American Pacific corophiid amphipods commenced with William Stimpson's (1857) description of *Corophium spinicorne* and *C. salmonis* from San Francisco Bay and Puget Sound. Knowledge of the biology of the two species in Central California was extended by Bradley (1908). In a pioneering series of systematic accounts, C. R. Shoemaker (1934a, 1941, 1949, 1955), described all seven remaining species known to be endemic to the eastern North Pacific region, from Alaska to Central America. Taxonomic features and range extensions of these and several introduced species were extended chiefly by J. L. Barnard (1952, 1954,

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1958, 1962, 1964, 1969b, 1973), Carlton (1979, 1985), Coyle & Mueller (1981), Austin (1985), Cadien (1991) and Chapman (1988), the latter containing a description of a new species probably synanthropic from the western North Pacific. Further, popular and semi-popular works by Ricketts and Calvin (1948), Aldrich (1961), Barnard (1975), Otte (1976), and Staude (1987) expanded knowledge of the ecology and life style of these mostly littoral and estuarine species, and provided illustrated keys to their identification. The systematics of species introduced from the North America Atlantic coast, or otherwise related to the North Pacific endemics, had been developed chiefly by Shoemaker (1934b, 1943, 1947), and Bousfield (1973), and that from western Europe mainly by Crawford (1937).

With respect to the corophiid fauna of the western North Pacific, Stimpson (1856) had briefly described the enigmatic *Corophium contractum* from the East China Sea and Sea of Japan, but the species was not recorded nor recognized subsequent to the world-wide compendium of Stebbing (1906). A few corophiid species were recorded from the far eastern USSR, mainly by Gurjanova (1951) and Kudrjaschov (1979), including a description of *Corophium steinegeri* Gurjanova from the Kamchatka Peninsula. Descriptions of new and introduced corophiid species from Japanese waters were initiated by Stephensen (1932), and continued by Irie (1958), Nagata (1965), Hirayama (1984, 1987a) and many others, all of which is usefully summarized by Ishimaru (1994). Hong (1983) and Kim (1991) treated the largely synanthropic corophiids of Korean coastal waters. A rich fauna of mainly primitive burrowing corophiids was described from coastal waters of the East China and South China Seas mainly by Yu (1938), Shen (1955), Ngoc (1965), Zhang (1974) and Hirayama (1986).

Despite these relatively recent and intensive studies, a significant hiatus in knowledge of corophiid amphipods of the northeastern Pacific region remained. The primary purpose of this study was therefore to treat the sytematics and distributional ecology of this little known fauna, based mainly on extensive regional survey material of the senior author since 1955, now contained in the crustacean collections of the CMN (Canadian Museum of Nature) in Ottawa. However, as discussed below (p. 69), new taxonomic insights revealed by the initial investigation, and attempts to place the fauna in a global context, necessitated expansion of its scope to a semi-phyletic revison of the genus *Corophium* Latreille, 1806, sens. lat. and its elevation to subfamily status.

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SYSTEMATICS

COROPHIIDAE Dana, 1849

Corophiidae Dana, 1849: 139.—Stebbing, 1906: 662 (part).—Gurjanova, 1951: 944 (part).—Barnard, 1969a: 184 (part).—Barnard, 1973: 17 (part).—Bousfield, 1973: 198 (part).—Lincoln, 1979: 520 (part).—Myers, 1982: 185 (part).—Ishimaru, 1994: 35 (part).
Corophioidea Barnard & Barnard, 1983: 220 (part).—Barnard & Karaman, 1991: 137.

Type Genus. *Corophium* Latreille, 1806, monotypy.

Genera. Corophiinae, new subfamily (p. 70.): *Corophium* Latreille, 1806 (sens. lat.).

Siphonoecetinae*: *Siphonoecetes* Kroyer, 1845: 491; *Australoecetes* Just, 1983: 128; *Bubocorophium* Karaman, 1981: 19; *Borneoecetes* Barnard & Thomas 1984: 873; *Rhinoecetes* Just, 1983: 125; *Africoecetes* Just, 1983: 17; *Concholestes* Giles, 1888: 238; *Caribboecetes* Just, 1983:130; *Carocubanus* Ortiz & Nazabal, 1984: 5.

*(Full references provided in Just,1983).

Diagnosis. Body depressed, cylindrical. Urosome segments separate, fused in advanced taxa. Head, rostrum usually distinct, short; inferior antennal sinus large. Antenna 1 short, slender, lacking accessory flagellum. Antenna 2 large, pediform, often sexually dimorphic; segments 4 and 5 stout; flagellum short.

Upper lip notched below. Lower lip, inner lobes prominent; mandibular lobes various. Mandible, molar strong, incisor moderate; palp short, appearing 2-(rarely 3-) segmented; left lacinia 3-4-dentate. Maxilla 1, inner plate small, unarmed; outer plate with 7 apical spines. Maxilla 2 strong, inner plate lacks facial setae. Maxilliped, outer plate medial margin straight, setose or spinose; palp, dactyl short, weak.

Coxal plates 1-4 small, non-overlapping. Gnathopods 1 & 2 dissimilar, basically not sexually dimorphic. Gnathopod 1 weakly subchelate or simple; carpus elongate. Gnathopod 2 subchelate or simple, stronger than gnathopod 1; merus and carpus elongate and variously fused; carpus, hind (free) lobe very short or lacking.

Peraeopods 3 & 4, short, segments 2 and 4 broadened ("glandular"); segment 5 usually short. Peraeopods 5 & 6 subsimilar, segment 5 with posterior marginal hook spines; segment 6 and dactyl reversed. Peraeopod 7 elongate, dissimilar in form to 5 & 6; distal segments not reversed.

Pleon plates shallow. Pleopod peduncles strongly broadened medially; outer ramus shorter than inner. Uropods 1 & 2 variously modified; rami short, unequal. Uropod 3 short, uniramous. Telson short, broad. Coxal gills sac-like, on peraeopods 3(4)-6. Brood lamellae strap-like, margins with long setae.

Taxonomic commentary. Just (1983) summarized recent major reclassifications and generic inclusions of the Corophiidae. Subsequent to the basic or "classical" compendia of Gurjanova (1951) and Barnard (1969a), Just noted a general trend to increasing refinement of classification within superfamily Corophioidea and a more restricted concept of the family Corophiidae. Thus, Myers (1981) provided solid taxonomic basis for continued distinction of Isaeidae, Aoridae, Ischyroceridae and Corophiidae, and created Neomegamphopidae for several mainly tropical genera allied to Isaeidae; and Lincoln (1979) restricted British genera of Corophiidae to *Corophium* Latreille, *Siphonoecetes* Kroyer, and *Unciola* Say. *Unciola* (and allied genera) were removed from Aoridae (below), but in the world fauna of Corophiidae, Bousfield (1982) included the genera *Kamaka* Derzhavin, *Gaviota* Barnard (now *Ampelisciphotis* Pirlot), *Janice* Griffiths, and *Paracorophium* and related genera.

However, in his revision of the superfamily Corophioidea, Barnard (1973) departed from the previous views and combined Corophiidae, Photidae (now Isaeidae) and Aoridae within family Corophiidae, and recognized no subfamilies. Barnard and Barnard (1983) continued this classification as applied to freshwater genera and species. In further expansion of the "lumper" philosophy, Barnard and Karaman (1991) submerged Ischyroceridae and Neomegamphopidae within Corophiidae, but maintained separate recognition of one subfamily, Siphonoecetinae Just, 1983. The presumed basis for their decision was the difficulty of recognizing clearly defined taxonomic "break-points" between families in the presence of morphologically "intermediate" genera, and in constructing workable keys to separate families that would rigidly apply to all component taxa.

However, in view of the work of Lincoln (1979), Just (1983, 1988), Myers (1981, 1982), and the senior author (Bousfield, 1978, 1982, 1983; Bousfield and Shih, 1994), the present authors cannot justify subordinating or fusing higher taxa on the basis that one (or a few) component lower taxa may appear "intermediate" in some character states. As opined elsewhere (Bousfield, 1983), Darwin's theory of biological evolution implies the existence of intermediate stages between all living organisms at one time or another. The taxonomic convenience of modern classification at family and subfamily level within valid (natural) superfamily concepts is not facilitiated by inability to treat, in a pragmatic manner, the so-called internal "exceptions". Cladistic and cluster analyses (Sneath & Sokal, 1973), and use of multiple-character diagnoses and "best-fit" criteria (Bousfield, 1983), provide more than adequate methodologies for treating such problems more realistically. We therefore continue to recognize family Corophiidae Dana as a natural family unit, here restricted to two component subfamilies, Siphonoecetinae and Corophiinae, as defined and keyed below. Subfamily Cerapiinae Budnikova, is removed to family Ischyroceridae. The present systematic treatment of the Corophiinae follows, in numerical analytical fashion, a revision of the Siphonoecetinae by Just (1983, et seq.), wherein similar numbers of species and global distributions are involved.

Taxonomic exclusions. The present authors have followed Myers (1981, 1982); Conlan (1983, 1991), Ishimaru (1994) and several other recent authors in continued separate recognition of families Aoridae, Isaeidae, and Ischyroceridae within superfamily Corophioidea. Aorids are characterized mainly by: the dominance of gnathopod 1 and peraeon 1 (in both males and females), an elongate antenna 1 with accessory flagellum, a generally non-pediform antenna 2 (male) and the use of gnathopod 1 in pre-amplexing (mate-guarding) behaviour. Lincoln (1979) also validated the family Corophiidae but included the genus *Unciola* Say, 1818. However, *Unciola* appears more naturally included within family Aoridae, as defined by Myers (1988), because it conforms with the major aorid character states (above). Moreover, the mouthparts are regular and unmodified; the bases of peraeopods 3 & 4 are of minimum "glandular" form and segments 4 & 5 normal; segment 5 of peraeopods 5 & 6 is not reduced nor does it bear hook spines; peraeopod 7 is not elongate and differs little in form or size from peraeopods 5 & 6; the pleopod peduncles are not expanded medially; uropods 1 & 2 are regularly linear; the telson is a simple plate without dorsal hooks; the brood lamellae are broad; and some peraeon segments bear a sternal spinose process (lacking in true corophiids).

KEY TO SUBFAMILIES OF COROPHIIDAE

1. Antenna 2 (male), segments 4 & 5 processiferous, often sexually dimorphic; uropods 1 & 2 inner ramus not markedly shortened; gnathopod 2, merus elongate; fused to elongate carpus .... Corophiinae (p. 70)

—Antenna 2, peduncular segments 4 & 5 not processiferous, little sexually dimorphic; uropods 1 & 2, inner ramus reduced or lacking; gnathopod 2, carpus short, deep, with free hind lobe ..... Siphonoecetinae Just

Ischyrocerids are fairly reliably distinguished from corophiids in their overlapping coxae 1-4; strongly setose filter-feeding antennae; antenna 1 with accessory flagellum; gnathopod 2 strongly subchelate (male) used in pre-amplexing mate-guarding; pleopod peduncles little broadened; and uropod 3, ramus with terminal hook spines. Isaeids (photids) are similar but generally deeper bodied, with deeper coxal plates, and uropod 3 is typically biramous and lacks terminal hooks. The genera *Paracorophium*, *Chaetocorophium,* and *Stenocorophium* exhibit several corophiin character states such as a weakly subchelate gnathopod 1 and elongate and setose merus of gnathopod 2, but are here considered essentially isaeid in form of antennae, deep coxae 1-4, unmodified pleopods, linear uropods, and overall morphology. Moreover, component species are antiboreal in distribution, remote from clusters of primitive corophiin genera.

COROPHIINAE, new subfamily

Corophium Latreille, 1806 (sens. lat.).—Stebbing, 1906: 662.—Gurjanova, 1951: 974.—Barnard, 1969a: 190.—Barnard, 1973: 17.—Bousfield, 1973: 198.—Lincoln, 1979: 522.—Barnard & Barnard, 1983: 162.—Barnard & Karaman, 1991: 184.—Ishimaru, 1994: 35.
Corophiinae (informal category) Just, 1983: 120.

Type genus. *Corophium* Latreille, 1806.

Genera of component subgroups.
1. Urosome segments unfused:
Eocorophium, new genus (p. 75); *Sinocorophium*, new genus (p. 75); *Corophium* Latreille, 1806 (p. 85); *Medicorophium*, new genus (p. 82); *Americorophium,* new genus (p. 90); *Chelicorophium,* new genus (p. 88).
2. Urosome segments fused: *Microcorophium*, new genus (p. 98); *Lobatocorophium*, new genus (p. 100); *Hirayamaia,* new genus (p. 108); *Crassicorophium,* new genus (p. 102); *Monocorophium*, new genus (p. 111); *Apocorophium,* new genus (p. 123); *Laticorophium,* new genus (p. 125).

Diagnosis. Body slender, elongate, smooth, depressed. Head broad, weakly rostrate. Urosome segments trending to fusion. Antenna 2 large, pediform, usually sexually dimorphic, with spines and processes for ambulation, burrowing (female and subadults) or mate guarding (adult males).

Mandibular palp, distal segment slender but distinct; proximal segment formed by fusion of embryonic segments 1 & 2, and distally bearing a single median plumose seta. Maxilliped, inner plate short, narrowing distally, apex setose; outer plate, inner margin setose, lacking masticatory spade spines.

Coxae 2-4 smaller and shallower than coxa 1; coxa 1 with 3-4 setae arising from subacute anterior corner. Gnathopods strongly dissimilar. Gnathopod 1 weakly subchelate. Gnathopod 2 simple; merus and carpus elongate, fused medially, bearing numerous filter setae that, with those of the opposing gnathopod, form a food-filtering basket.

Peraeopods 3 & 4, basis linear to inflated and glandular; segment 4 often broadened anterodistally; segment 5 variously shortened. Peraeopods 5 & 6 subsimilar in form, 6 distinctly the larger; segment 5 bearing 2 posterolateral clusters of hooked spines; segment 6 and dactyl usually reversed. Peraeopod 7 elongate, ambulatory, margins of basis strongly plumose-setose.

Pleon plates rounded or squared behind, seldom acuminate. Pleopods short, strong; peduncles deep, strongly broadened medially. Uropods 1 & 2 regular, subequally biramous, rami spinose mainly or exclusively on outer margin. Uropod 3, ramus sublinear or broadened, often not longer than the peduncle, distally setose. Telson free, with subapical dorsal spinules.

Coxal gills on peraeopods 3-6. Brood plates large, strap-like, with long marginal setae.

Distributional ecology: Essentially holarctic in temperate and warm temperate littoral and sublittoral shelf waters; dominant in the North Pacific; overlapping with Siphonoecetinae mainly in the North Atlantic-Mediterranean region; several species (of advanced tube-builders) are widely synanthropic, including the Southern Hemisphere.

Behaviour. Corophiins are primarily burrowers in fine soft sediments, using antennae, peraeopods 3 & 4, and uropods, aided by water currents set up by the powerful pleopods. More advanced species live in fixed open-ended abodes cemented to solid bottom objects. Some species (e.g., *Corophium insidiosum*) can do both (Stock, 1952). Animals crawl slowly along the bottom using antenna 2, peraeopod 7, and uropods. . Advanced corophiids are adept at reversing their bodies quickly within the tube and are thereby able to face into the intermittently reversing tidal currents or confront unwelcome intruders at the rear of the tube.

By contrast, siphonoecetins do not burrow, but form mobile abodes by cementing together tiny mollusk shells and/or relatively coarse sediments. Both sexes may crawl slowly by means of their powerful ambulatory antenna 2,

dragging their abodes with them (Just, 1988). Males may cement the abodes of one or more females to their own, all facing in the same direction which, not being fixed, can be turned about to face reversing feeding currents. Antenna 2 is employed in a flipping action in some highly mobile species. In corophiins, however, antenna 2 is strongly pediform in the male, the distal segments with specialized processes that serve in mate-guarding and holding the female during amplexus (Conlan, 1991).

Just (1983, p. 120) opined that *Corophium* (then with some 50 species) (is a) "logical sister group [for Siphonoecetinae, new subfamily]" and "a candidate for subfamily ranking", but he hesitated to formally recognize it as such. Although the present authors have examined material of only half the genera newly proposed, classificatory decisions are to large extent based on the excellent taxonomic accounts and figures provided by previous authors, including Shoemaker (1947, 1949), Barnard and Karaman (1991), Lincoln (1979), Myers (1982), and Hirayama (1984, 1986, 1987a). We now believe Just's reservations are largely "put to rest" in the following considerations and have herewith fulfilled his initial suggestion in formally proposing Corophiinae, new subfamily.

CHARACTERS AND CHARACTER STATES

Taxonomic and classificatory analysis of subfamily Corophiinae is based mainly on characters and character states illustrated in Figs. 1 & 2 (pp. 72-73). The plesiomorphic state is shown in the left-hand column, the apomorphic state in the right-hand column, and a representative intermediate state (when suitable) in the middle column. As in previous numerical analyses of this type (e. g., Bousfield & Chevrier, 1996), the three character states are given phyletically ordered values of 0, 2 and 1, respectively (see also pp. 130-133, Fig. 38, and Table I, this paper).

The following commentary elucidates the illustrations. The lower margin of the inferior antennal sinus (1) is plesiomorphically projecting, apomorphically strongly regressed. Antenna 1 (2) is plesiomorphically slender, peduncular segments elongate, unmodified, and flagellar segments numerous; apomorphically it is relatively short, the peduncular segments variously thickened, spinose or setose, and flagellar segments few. In antenna 2 (male) (3, 4, 5), plesiomorphically the gland cone is elongate and/or prominent, segment 4 is moderately thickened, the distal process is small and single toothed (or lacking), segment 5 lacks a median marginal tooth, the distal process is small (or lacking), and the flagellum is relatively long and slender; apomorphically the gland cone is short or inconspicuous, segment 4 is broad (stout), the distal process is large and bidentate, segment 5 has strong median and distal processes, and the flagellum is short and thick. In antenna 2 (female of sexually dissimilar species) (6), the gland cone is large, peduncular segments 4 & 5 are slender, little modified, and the flagellum is slender; apomorphically, the gland cone is inconspicuous, peduncular segments 4 & 5 are short, thick, and marginally spinose, and the flagellum is short. In antenna 2 of a sexually similar female or hermaphrodite (7), plesiomorphically, as in the male (3-5, above); apomorphically, the appendage is much less stout, the distal process of segment 4 is single-toothed, and segment 4 lacks median and distal processes.

The lower lip (9) plesiomorphically has very short mandibular lobes; apomorphically the lobes are strong, distinct. The mandibular palp (8) plesiomorphically consists of two apparent segments aligned linearly (the proximal segment is composed of the two fused primary segments that are occasionally not fused) (Type P1 of Hirayama, 1987b); apomorphically the distal segment is set at an angle to the proximal segment which bears a terminal seta on a triangular prominence (Type P5 of Hirayama, 1987b). In the primitive maxilliped (10), the inner plate is relatively large, with numerous marginal setae, the outer plate large, and palp segment 2 elongate; in the apomorphic condition, the inner plate is short, with few marginal setae, the outer plate small, and palp segment 2 short, little longer than segment 1.

In gnathopod 1 (11), the propodal palm is plesiomorphically distinct, vertical, little exceeded by the simple short dactyl; apomorphically, the palm is short, oblique, distinctly exceeded by a dactyl that may bear a posterior marginal denticle. In gnathopod 2 (12), the dactyl is plesiomorphically simple and strong; apomorphically it is short, with 2-4 posterior marginal teeth; in the intermediate condition the dactyl bears a single posterior marginal tooth, and the propod bears a distinct posterodistal cusp.

In peraeopods 3 & 4 (13, 14), plesiomorphically the basis is slender, segment 4 is little expanded distally, segment 5 is subequal in length to 4, and the dactyl is elongate; apomorphically, the basis is broad and glandular, segment 4 is broadened distally and overhangs the short segment 5 , and the dactyl is shorter than segment 6. In peraeopods 5 & 6 (15, 16), plesiomorphically the basis is little broadened, segment 5 is not shortened, the posterodistal "hook spines" are elongate, and segment 6 and dactyl are not reversed; apomorphically, the basis is broadened, segment 5 is very short, with short hook spines, and segment 6 and dactyl are reversed. Peraeopod 7 (17) is plesiomorphically elongate, with narrow basis and elongate dactyl; apomorphically it is relatively short, the basis broadened, and the dactyl short and curved.

In pleon plate 3, plesiomorphically the hind corner (18) is produced and acute, but apomorphically broadly obtuse or rounded, and weakly acuminate or squared in the intermediate condition. In the urosome (19), pleisomorphically the segments are separate, with sharp notches for full lateral insertion of uropod 1; apomorphically, the segments are totally fused,the lateral margins convex, and uropod 1 is inserted ventrally; in the intermediate condition, the segments are fused, the notch is shallow, the lateral margin is straight or incised, and uropod 1 is inserted partly ventrally. In uropod 3 (20), the ramus is apomorphically slender, elongate and spinose, and the peduncle lacks a lateral process; apomorphically, the ramus is short, suborbicular, and the peduncle usually bears a lateral process. Character states of other appendages (e .g., coxal gills, brood plates, and pleopod peduncles) have also been considered in the analysis.

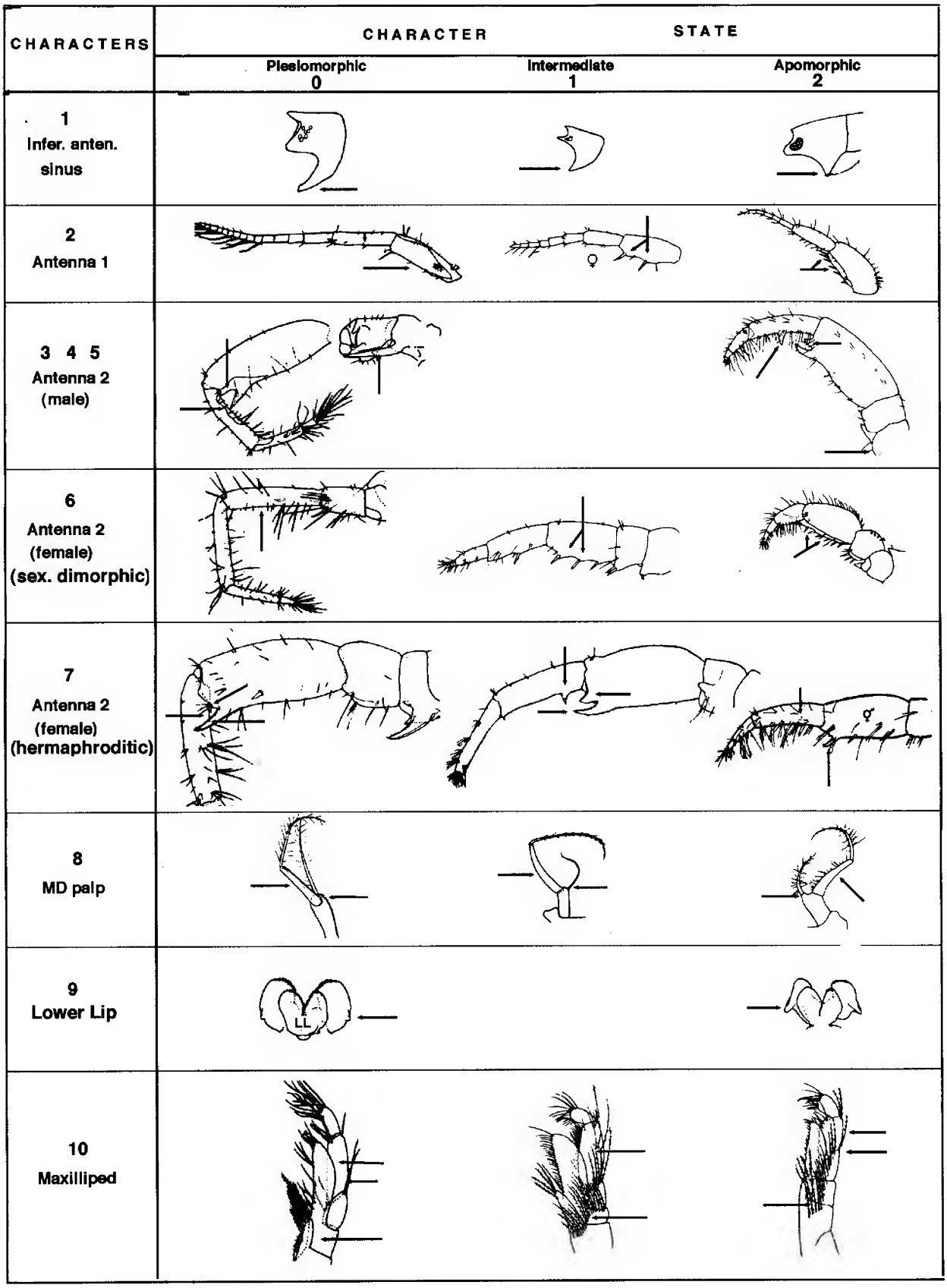

FIG. 1. CHARACTERS AND CHARACTER STATES OF GENERA OF COROPHIINAE.

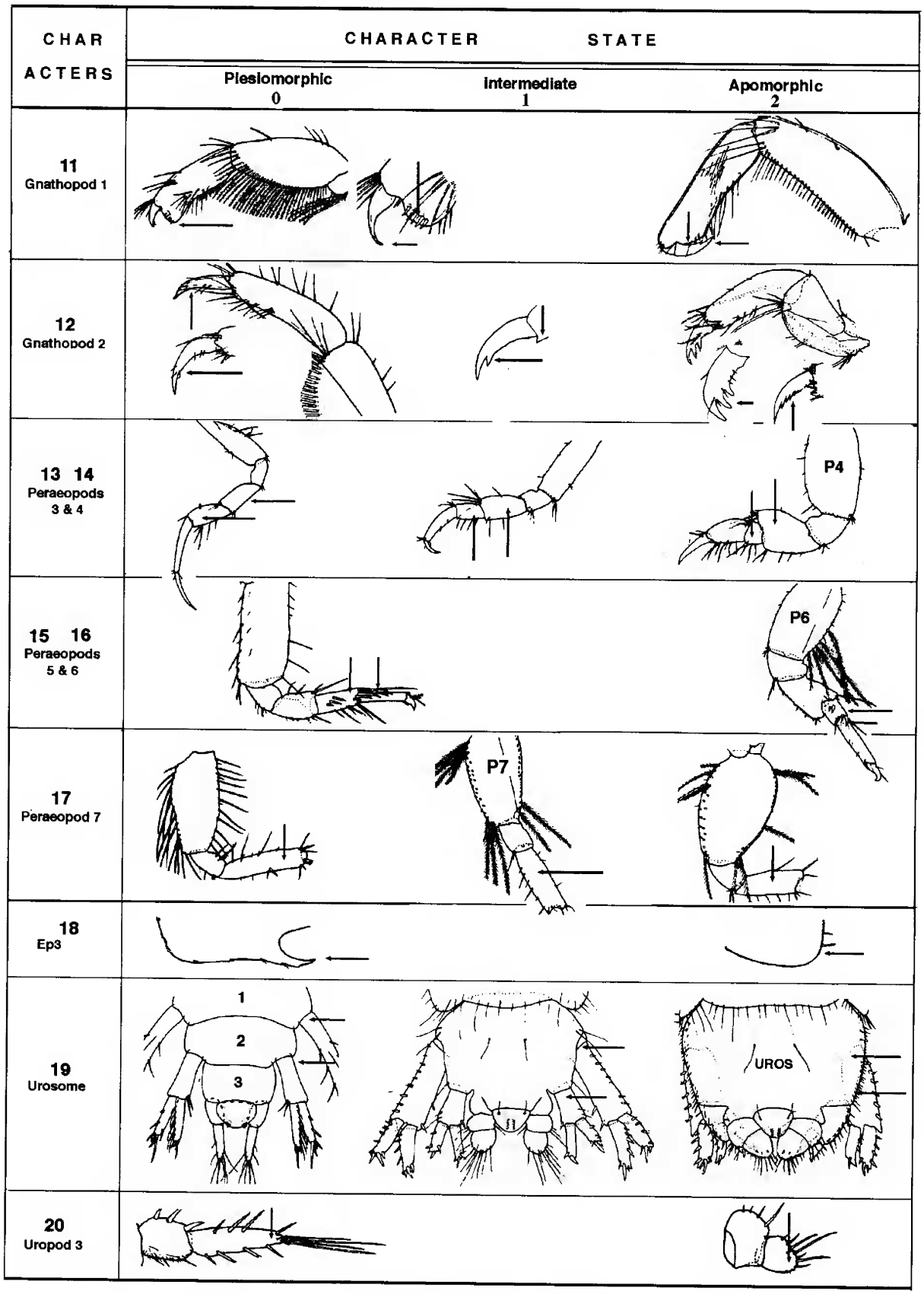

FIG. 2. CHARACTERS AND CHARACTER STATES OF GENERA OF COROPHIINAE (cont.)

KEY TO WORLD GENERA OF COROPHIINAE

1. Urosome segments separate (except *C. ellisi*), uropod 1 variously laterally inserted (Fig. 2:19 P) . . . . . 2.

—Urosome segments fused; uropod 1 often partly or totally ventrally inserted (Fig. 2:19 A) . . . . . 7.

2. Antenna 2, gland cone of segment 2 large, conspicuous (Fig. 1: 3 P); maxilliped palp segment 2 elongate (Fig. 1: 10 P) . . . . . 3.
—Antenna 2 gland cone small to medium, not prominent (Fig. 1: 3 A); maxilliped palp segment 2 short to medium (Fig. 1: 10 A) . . . . . 6.

3. Pleon plate 3, hind corner strongly produced, acute (Fig. 2:18 P) . . . . . *Eocorophium*, n. g. (p. 75)

—Pleon plate 3, hind corner rounded, subquarate or weakly acuminate (Fig. 2:18 A). . . . . 4.

4. Peraeopods 3 & 4, segment 5 shortened (<< segment 4) (Fig. 2:14 A) . . . . . 5.

—Peraeopods 3 & 4, segment 5 not shortened (~ segment 4)(Fig. 2:14 P). . . . . *Sinocorophium,* n. g. (p. 75)

5. Uropod 3, ramus short, broad, little longer than peduncle .(Fig. 2:19 I) . . . . . *Corophium* Latreille (p. 85)

—Uropod 3, ramus slender, longer than peduncle ..(Fig. 2: 19 P) . . . . . *Medicorophium,* n. g. (p. 82)

6. Uropods 1 & 2, rami with medial spines (setae) (Fig. 2:12 U1, U2): antenna 2 powerful, similar in both sexes, segment 4 and flagellum short (Fig. 1: 4, 5 A); Aralo-Caspian.. . . . . *Chelicorophium* , n. g. (p. 88)
—Uropods 1 & 2, rami lacking medial spines or setae (Fig. 17:UROS); antenna 2 usually sexually dissimilar (Fig. 1: 6 I) (includes *C. ellisi* with urosome segments fused); American-Atlantic and eastern N. Pacific . . . . . .*Americorophium* (p. 90)

7 Urosome segments with strong lateral notch for mainly lateral insertion of uropod 1 (Fig. 2:19 I) . . . 8.

—Urosome segments, lateral notches weak or lacking, uropod 1 arising mainly ventrally (Fig. 2:19 A) . 10.

8. Peraeopods 3-4, basis and segments 4 & 5 slender (FIG. 2:13 P) . . . . . *Microcorophium* , n. g. (p. 98)

—Peraeopods 3-4, basis and segments 4 & 5 variously broadened, "glandular" in form (Fig. 2:13 A). . . . 9.

9. Gnathopod 2, dactyl with 2-3 posterior marginal teeth (Fig. 2:12 A); mandibular palp segment 1 with unproduced distal shelf (Type P4) (Fig. 1:8 I) . . . . . *Monocorophium,* n. g. (p. 111)

—Gnathopod 2, dactyl with single posterior marginal tooth (Fig. 2:12 I); mandibular palp with distal process (Type P5) Fig. 1: 8 A) . . . . . *Crassicorophium* , n. g. (p. 102)

10. Uropod 2 large, broad, larger than uropod 1 (FIG. 25:UROS). . . . . .*Lobatocorophium,* n. g. (p. 100)

—Uropod 2 relatively inconspicuous, distinctly smaller than uropod 1 (Fig. 2:19 I, A). . . . . 11.

11. Urosome, lateral margins straight or slightly indented (Fig. 24:UROS); gnathopod 2, propod with minute palm and cusp; dactyl with 1(2) posterior marginal tooth (Fig. 2:12: I) . . . . . *Hirayamaia,* n. g. (p. 108)

—Urosome, lateral margins convex (FIG. 2:19 A); gnathopod 2, propod lacking palm or minute cusp; dactyl with 2-4 posterior marginal teeth. (Fig. 2:12 A). . . . . 12.

12 Urosome, lateral margins smooth (Fig. 2:19 A) . . . . . .*Apocorophium* , n. sp. (p. 123)

—Urosome, lateral margins each with small notch .(Fig. 37:UROS) . . . . . *Laticorophium* , n. sp. (p. 125)

***Eocorophium*, new genus**
(see Fig. 3)

Corophium Latreille, Hirayama, 1986: 449 (part: *C. kitamori* Nagata).—Barnard & Karaman, 1991: 184 (part).—Ishimaru, 1994: 35(part).

Type species. *Corophium kitamori* Nagata, 1965 (monotypic)

Diagnosis. A primitive genus, endemic to Hong Kong regional waters. Urosome segments unfused. Uropods arising from lateral notches. Head, rostrum short, broad; inferior antennal sinus with anteriorly directed lower margin. Antenna 1 short; peduncular segment 3 medium. Antenna 2 pediform in male (slender, unlike in female); gland cone elongate; segment 4 with single posterodistal process; segment 5 with strongly developed apical process, but median tooth lacking; flagellum medium, 3-segmented, shorter than peduncle 5, apex lacking curved spines.

Mouthparts basic. Upper lip, epistome produced. Lower lip, mandibular lobes very short. Mandibular palp of type P3 (fide Hirayama, 1987b). Maxilla 1, inner plate broad; palp broadened distally. Maxilla 2, plates narrow. Maxilliped, inner plate short, blunt, strongly setose; outer plate slender, inner margin intermittently setose; palp segment 2 slender, elongate.

Gnathopod 1, carpus and propod subequal in length; palm short, oblique; dactyl strong exceeding palm. Gnathopod 2, fused merus and carpus longer than propod; dactyl thin, elongate, simple.

Peraeopods 3 & 4, segments linear; segment 4 not shortened. Peraeopods 5 & 6, basis not broadened, segment 5 not shortened, with elongate posterodistal spines; segment 6 and short dactyl not reversed. Peraeopod 7 slender, elongate, dactyl moderately long.

Pleon plate 3, hind corner acutely produced. Pleopod peduncles little broader than long. Uropod 1, peduncle linear, slender; rami linear, margins spinose, apex with long spines. Uropod 2 not shortened; rami linear, margins and apex spinose. Uropod 3, ramus linear, elongate, margins spinose. Telson rounded, lacking dorsal spines.

Coxal gills short, sac-like, on peraeopods 2- 6. Brood lamellae undescribed.

Etymology. From the Greek "eo" - dawn or early, and the generic root *Corophium*, with reference to the plesiomorphic nature of its generic character states.

Distribution. Endemic to the Sea of Japan and East China Sea, western North Pacific region.

Taxonomic commentary. *Eocorophium* is remotely allied to the western North Pacific cluster of *Sinocorophium* via species such as *C. sinense*. Hirayama (1986, 1987a) considers this species to represent a distinct evolutionary branching pathway within *Corophium* sens. lat. Such appears convergently similar to *Stenocorophium* Karaman, 1979, within the Isaeidae. Thus, because of the autapomorphic form of gnathopod 2 in *Stenocorophium* and the plesiomorphic form of its coxal plates, antennae, uropod 3, etc., *Stenocorophium* is an unlikely candidate for direct ancestry to *Eocorophium*.

***Sinocorophium*, new genus**
(see Figs. 4, 5)

Corophium Latreille, Hirayama, 1986: 449 (part).—Hirayama, 1987a: 175 (part).—Hirayama, 1987b: 569 (part).—Barnard & Karaman, 1991: 185 (part).—Ishimaru, 1994: 35 (part).

Type species. *Corophium sinensis* Zhang, 1974 (present designation).

Species. *Sinocorophium heteroceratum* (Yu, 1938); *S. lamellatum* (Hirayama, 1984); *S. minutum* (Ngoc, 1965); *S. homoceratum* (Yu, 1938); *S. triangulopedarum* (Hirayama, 1986); *S. intermedium* (Ngoc, 1965); *S. alienense* (Chapman, 1988); *S. japonicum* (Hirayama, 1984, new status); *S. monospinum* (Shen, 1955).

Diagnosis. Urosome segments uncoalesced. Head, rostrum distinct; inferior lateral sinus large, regressed below. Antenna 1 elongate (usually exceeding antenna 2, peduncular segment 4); peduncular segment 3 shortened (<1/2 segment 2). Antenna 2 strong, pediform (often subsimilar in female), segment 4 with simple (occasionally bifid) posterodistal tooth; segment 5, median tooth and posterodistal process lacking (or weak); flagellum 2-3-segmented, shorter than peduncular segment 5; gland cone large, prominent.

Mouthparts basic. Upper lip, epistome produced, acute. Lower lip, mandibular lobes small. Mandibular palp basic (types P1, P1r of Hirayama, 1987b). Maxilla 1, palp longer than outer plate. Maxilliped, inner plate, apex rounded, setose; outer plate broad, inner margin variously setose; palp segment 2 elongate, often broadened, outer margin with long filter setae.

Gnathopod 1 primitively subchelate; palm of propod short, vertical; dactyl short. Gnathopod 2, merus not occluding distal free margin of carpus; dactyl large, simple.

Peraeopods 3 & 4, basis sublinear; segment 4 little broadened distally, segment 5 little (or not) shorter than 4; dactyl medium, curved. Peraeopods 5 & 6, bases little broadened, posterior margin (especially of P6) setose, segment 4 long, with anterodistal lobe; segment 5 distinct, posterodistal spines elongate; segment 6 and dactyl not reversed. Peraeopod 7 elongate, basis little broadened; dactyl long.

Pleon plate 3, hind corner acuminate or squared. Pleopod peduncles little broader than deep. Uropod 1, rami sublinear, inner ramus the shorter. Uropod 2 not shortened, rami linear, both margins spinose. Uropod 3, ramus linear to subovate, usually longer than peduncle. Telson short, subtriangular.

Coxal gills medium, slender sac-like, on peraeopods 3-6. Brood lamellae medium, marginal setae short.

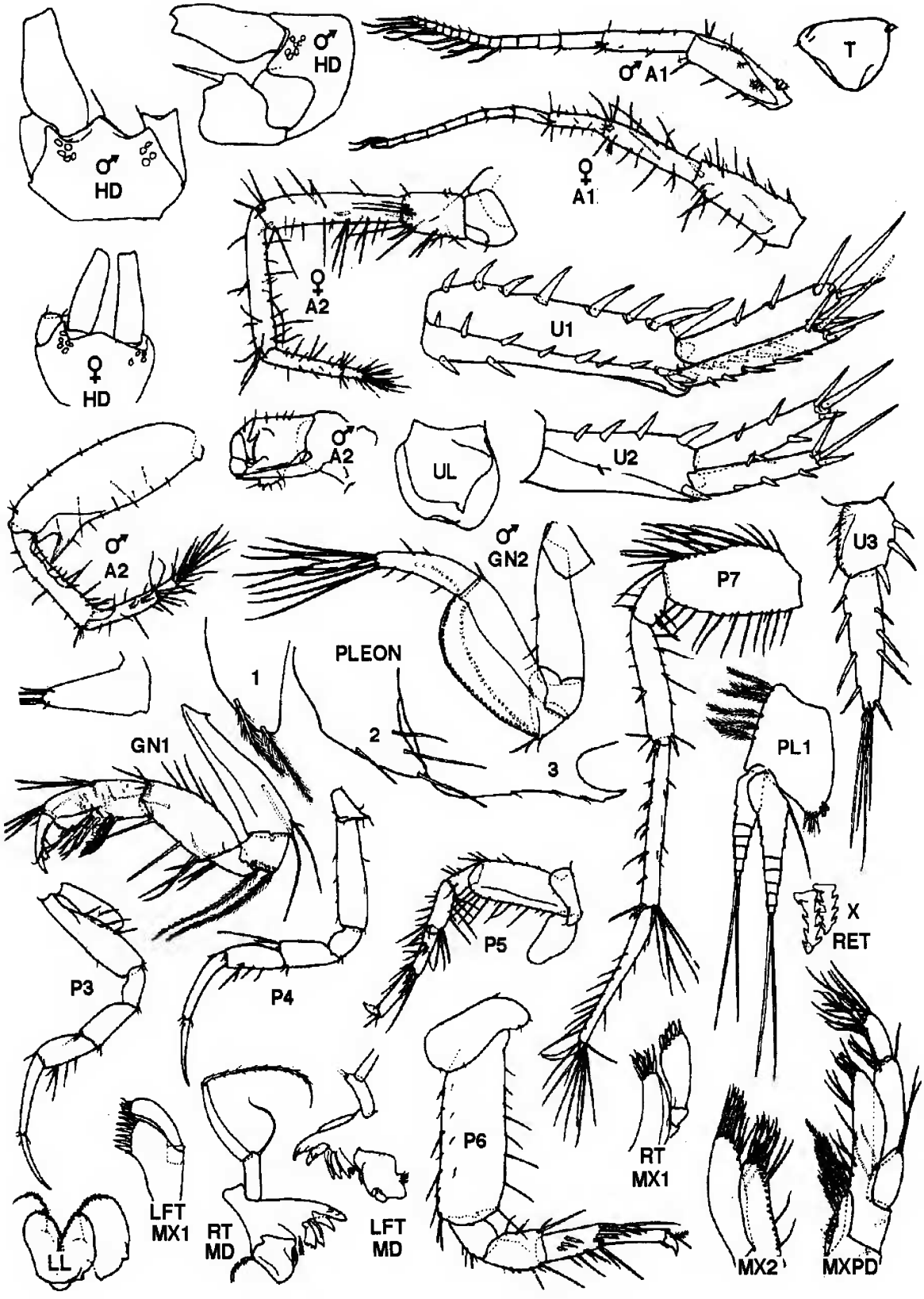

FIG. 3. ***Eocorophium kitamori*** **(Nagata, 1965). South China Sea (after Hirayama, 1986).**

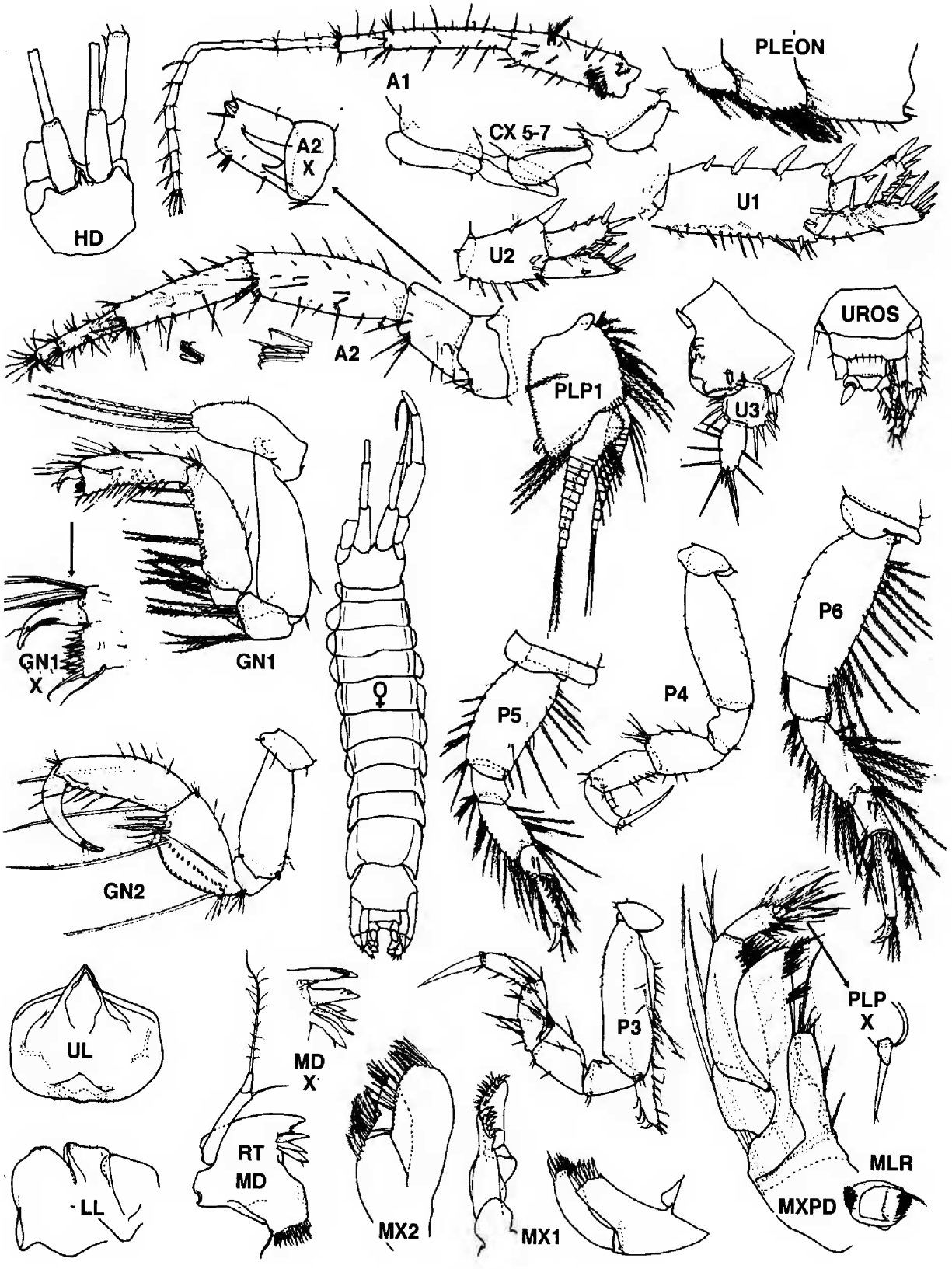

FIG. 4. ***Sinocorophium sinense*** **(Zhang). Seto Inland Sea. Female (6.5 mm) (after Hirayama, 1987a).**

KEY TO NORTH PACIFIC SPECIES OF *SINOCOROPHIUM*

1. Antenna 2 sexually dimorphic, pediform in male only; gnathopod 1 subchelate, palm nearly vertical; peraeopods 3 & 4, segment 5, length ~segment 4; uropod 3, ramus sublinear, longer than peduncle . . . 2.
—Antenna 2 sexually subsimilar; gnathopod 1 weakly parachelate, palm reverse-oblique; peraeopods 3 & 4, segment 5 relatively short, <2/3 length of segment 4; uropod 3, ramus short, broad . . . . 5.

2. Uropod 3, peducle with setose lateral process; mandibular palp, terminal segment very short . . . . . 3.
—Uropod 3, peduncle lacking distinct lateral process; mandibular palp, terminal segment normal . . . . . 4.

3. Antenna 1, peduncular segment 1 with posterior marginal process . . . . . *S. heteroceratum* (Yu)
—Antenna 1, peduncular segment 1 lacking posterior marginal process . . . . . *S. sinensis* (Zhang)

4. Gnathopod 1, propod broad, palm oblique; uropod 2, inner ramus fully spinose . *S. lamellatum* (Hirayama)
—Gnathopod 1, propod regular, palm vertical; uropod 2, inner ramus spinose laterally . . *S. minutum* (Ngoc)

5. Uropod 1, rami subequal in length, nearly straight . . . . . *S. intermedium* (Ngoc)
—Uropod 1, inner ramus short, curved medially . . . . . 6.

6.Antenna 2 (male), segment 4 with bidentate posterodistal process; maxilliped outer plate elongate, exceeding palp segment 2 . . . . . *S. homoceratum* (Yu)
—Antenna 2 (male), posterodistal process of segment 4 unidentate; maxilliped, outer plate medium, not reaching distal margin of palp segment 2 . . . . . 7.

7. Peraeopod 5, basis, posterior margin setose; gnathopod 2, dactyl long . . . . . *S. alienense* (Chapman) (p. 80)
—Peraeopod 5, basis lacking posterior marginal setae; gnathopod 2, dactyl medium . . . . . 8.

8. Uropod 3, ramus suborbicular in form, shorter than peduncle; peraeopods 3 & 4, posterodistal margin of basis with 1-2 long setae only . . . . . *S. triangulopedarum* (Hirayama)
—Uropod 3, ramus oblong, subequal to peduncle; peraeopods 3 & 4, basis with several posterodistal setae; . . . . . *S. japonicum* (Hirayama)

Etymology. A combining form of the Latin prefix "sino"- Chinese, and the generic root *Corophium*, with reference to the endemism of component species in the East China Sea and adjacent regions.

Distributional ecology. The ten described species are endemic to warm temperate and subtropical shallows of the southeastern Sea of Japan, East China Sea and the South China Sea, south to Vietnam, where they burrow in soft marine and brackish substrata. One species occurs synanthropically in San Francisco Bay.

Behaviour. Virtually nothing is known. All species are presumed to be free-burrowing, mainly in muddy substrata, the tubes of which may be lined with the cemented grains of the substratum. Males are presumed to mate-guard.

Taxonomic commentary. Within subfamily Corophiinae, *Sinocorophium* demonstrates mostly plesiomorphic character states that appear to link it with presumed ancestral isaeids such as *Paracorophium* on the one hand, and (less likely) *Kamaka* on the other. Its plesiomorphic character states (e .g., large antennnal gland cone, short mandibular lobes of the lower lip, elongate maxillipedal palp segment 2, linear uropod rami, elongate maxilliped palp segment 2) suggest closest phyletic relationship with the western European genus *Corophium,* linked by species of the Indian Ocean (e. g., *C. madrasensis*?).

Reasonable grounds for formal subgeneric treatment of species within *Sinocorophium* is provided by numerical taxonomic analysis (Fig. 39 p. 132). A relatively primitive subgroup might include *S. sinensis, S. heteroceratum, S. lamellatum,* and *S. minimum.* A more advanced assemblage includes *S. homoceratum, S. intermedium, S. triangulopedarum, S. japonicum, S. alienense,* and possibly *S. monospinum.* In the latter cluster of species, antenna 2 is not sexually dimorphic, segments 2 and 4 of paired peraeopods 3 & 4 and 5 & 6 are more "glandular" (broadened), the rami of uropods 1& 2 are more unequal, and spinose mainly on the outer margin, and the ramus of uropod 3 is relatively short and broad. Formal taxonomic recognition of these differences, however, awaits the collection and analysis of more extensive and more complete materials.

Corophium contractum Stimpson, 1856, was imperfectly described and is not distinguishable from more recent species with urosome segments fused. Since the type may have been lost in the great Chicago fire of 1871 (Manning, pers. comm.) and material has not been subsequently identified, the species is here considered a nomen nudum [Stebbing (1906) suggested it may have been a female of *C. bonelli*].

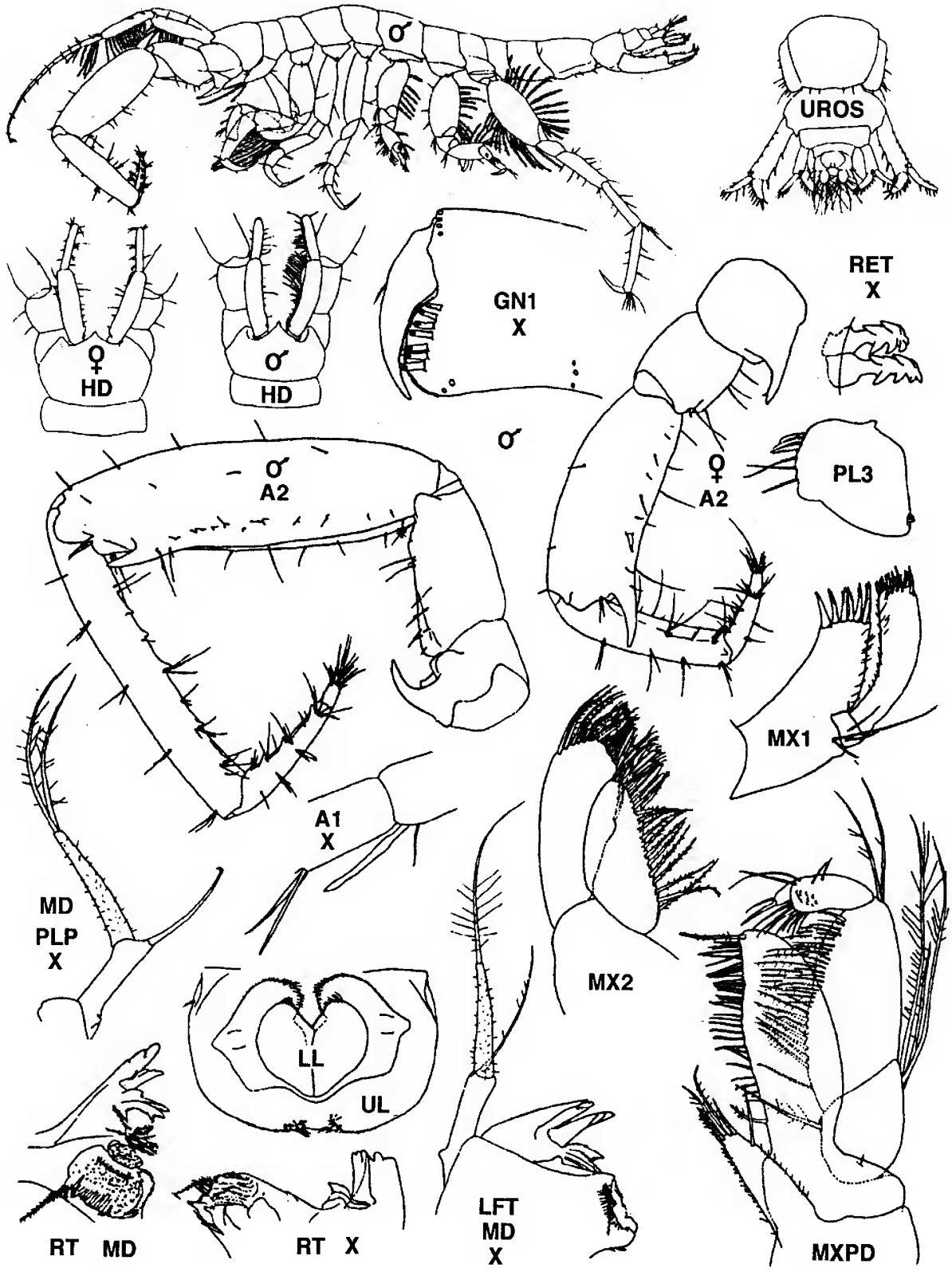

FIG. 5. *Sinocorophium alienense* (Chapman). San Francisco Bay. Male (6.5 mm); female (6.0 mm) (after Chapman, 1988).

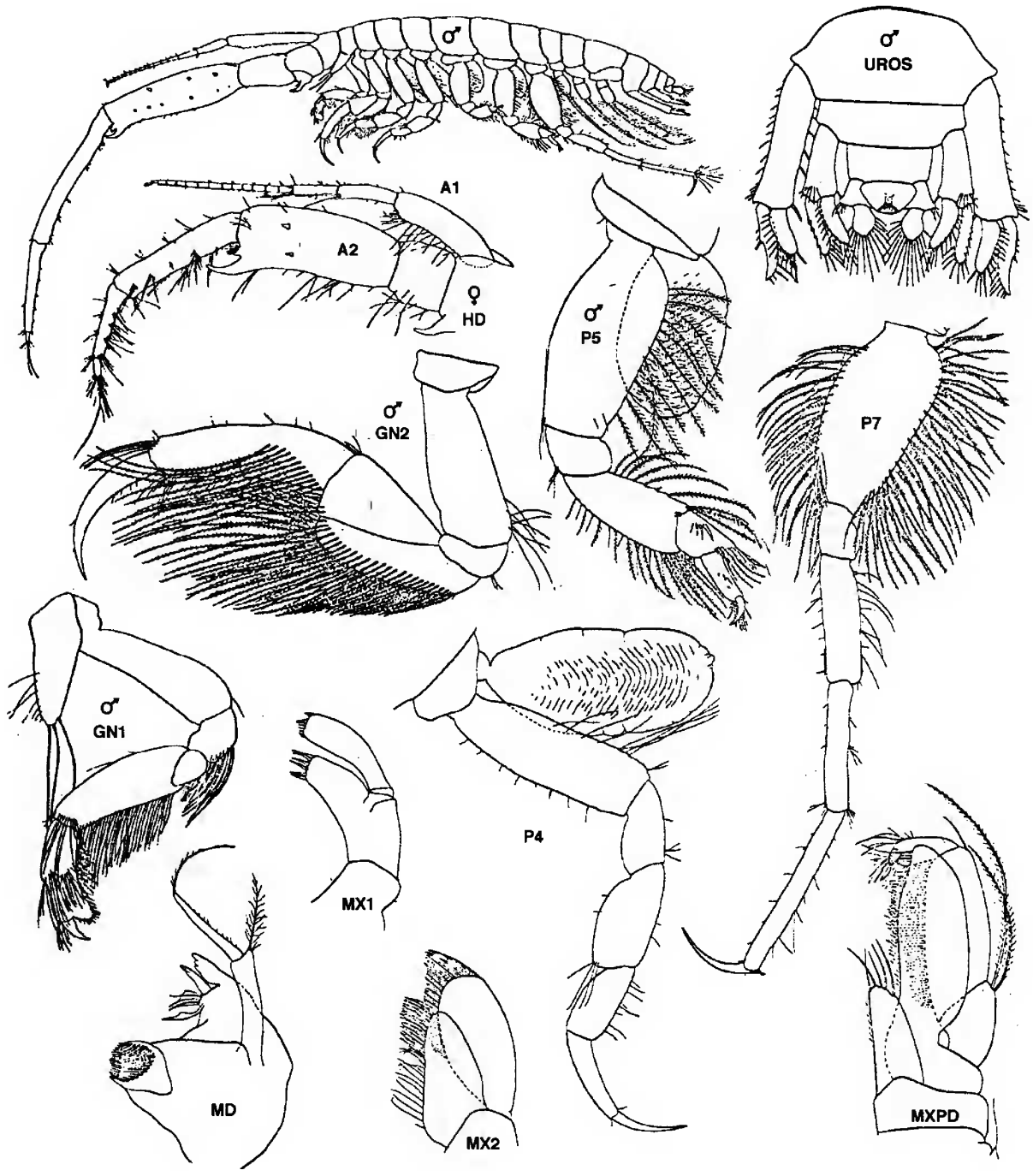

FIG. 6. Sinocorophium homoceratum (Yu). East China Sea. Male (10-12.0 mm); female (6.5 -9.5 mm) (after Yu, 1938).

Sinocorophium alienense (Chapman)
(Fig. 5)

Corophium alienense Chapman, 1988: 368, figs. 3-5.

Material examined. None from the study region.

Distributional Ecology. The species is unknown outside the San Francisco Bay area and is closely similar to *S. triangulopedarum* (Hirayama, 1986) and other species of the western North Pacific (key, p. 78). These factors led Chapman (loc. cit.) to conclude that the species is probably native to the western North Pacific and synanthropic in the eastern North Pacific.

Sinocorophium homoceratum (Yu)
(Fig. 6)

Corophium homoceratum Yu, 1938: 84, figs, 1-5.—Ngoc, 1965: 150, table I.—Barnard & Karaman, 1991: 185.

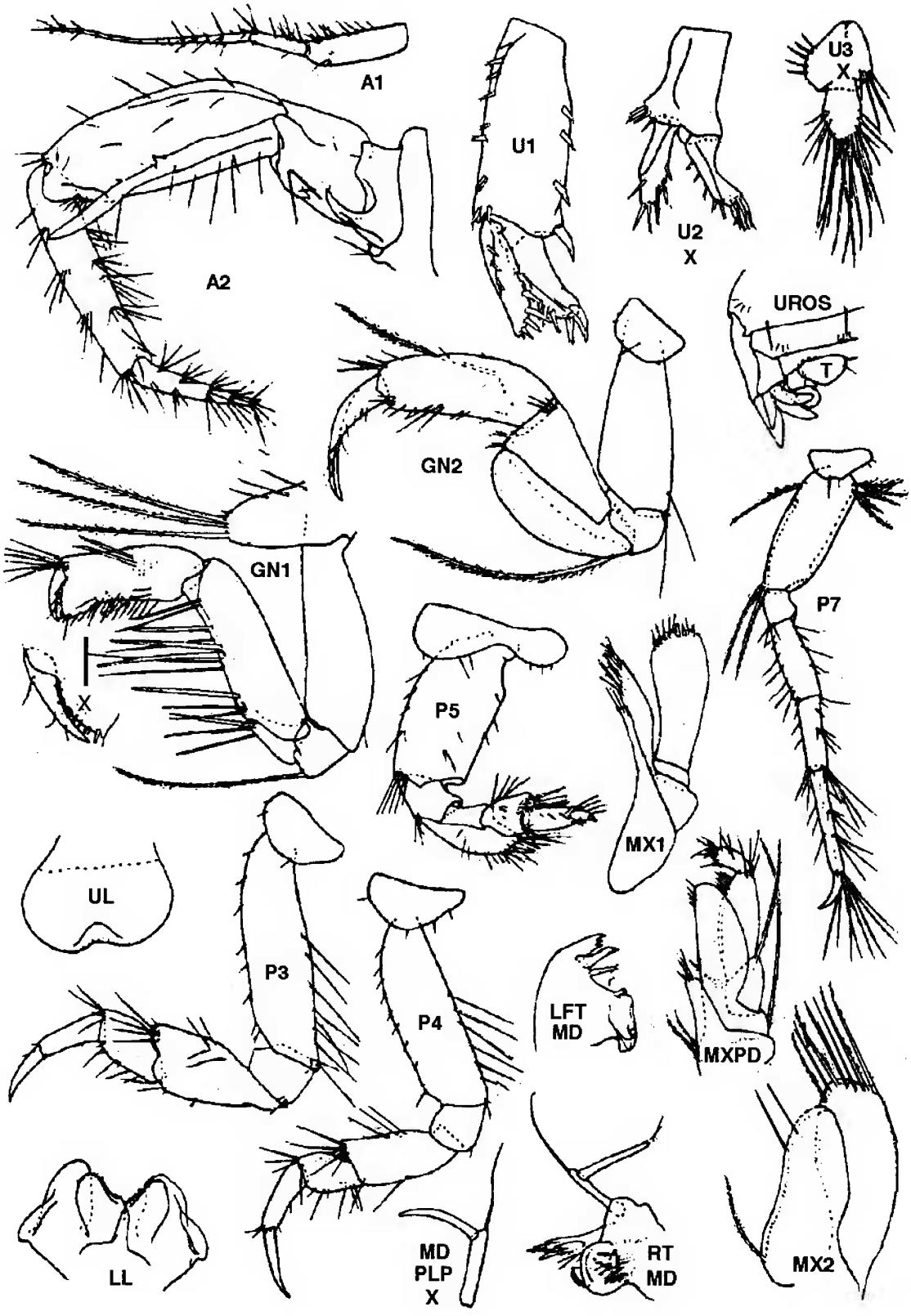

Fig. 7. ***Sinocorophium japonicum*** **(Hirayama). Tomioka Bay, Japan. Female (6.0 m) (after Hirayama, 1984).**

Medicorophium, new genus
(see Figs. 8, 9)

Corophium Latreille, 1806, Chevreux & Fage, 1925: 363 (part).—Crawford, 1937: 592 (part).—Gurjanova, 1951: 974 (part).—Myers, 1982: 185 (part).—Barnard & Karaman, 1991: 185 (part).

Type species. *Corophium aculeatum* Chevreux, 1908 (present designation).

Species. *Medicorophium rotundirostre* (Stephensen, 1915); *M. minimum* (Schiecke,1978); *M. annulatum* (Chevreux, 1908); *M. runcicorne* (Della Valle, 1893); *M. affine* (Bruzelius, 1859).

Diagnosis. Small to medium corophiids (1.5-6.0 mm). Urosome segments separate. Head, rostrum short or rounded; inferior sinus deep, regressed. Antenna 1 relatively elongate; segment 3 not shortened. Antenna 2 sexually dimorphic. Antenna 2 (male) pediform; segment 4 with single or bidentate distal process; segment 5, median tooth small or lacking, distal process lacking; gland cone medium strong.

Mouthparts incompletely known (limited for *M. rotundirostre*). Upper lip, epistome produced(?). Lower lip, mandibular lobes weak(?) Mandibular palp advanced (type P4-P5 of Hirayama, 1987b). Maxilla 1, palp not exceeding outer plate. Maxilliped, palp segment 2 elongate(?).

Gnathopod 1 very weakly subchelate; dactyl pectinate behind, overlapping short, oblique propodal palm. Gnathopod 2, merus fused along entire lower length of carpus; dactyl simple or weakly bidentate distally.

Peraeopods 3 & 4, basis and segment 4 little broadened; segment 5 short, little overhung by segemnt 4; dactyls slender, elongate. Peraeopods 5 & 6, basis little broadened; segment 4 short, little broadened anterodistally; segment 5 with weak, elongate, posterodistal spines; segment 6 and dactyl not reversed(?). Peraeopod 7 slender, elongate.

Pleon plate 3, hind corner rounded. Uropod 1, peduncle slender; rami straight, subequal, outer margin spinose, apices with long spines. Uropod 2 not reduced. Uropod 3, ramus slender, longer and narrower than peduncle. Telson broad, rounded, with dorsal hook spines.

Coxal gills slender, sac-like. Brood lamellae medium, sublinear (*M. runcicorne*).

Etymology. A combining form of the Latin prefix *medi* - middle, and the generic root *Corophium*, with reference to the Mediterranean-endemic nature of component species.

Distribution. Largely endemic to the Mediterranean and Black Seas, burrowing in fine sediments, littoral-sublittoral to depths of 80 m.

Taxonomic commentary. Crawford (loc. cit.) treated *M. aculeatum, M. annulatum, M. runcicorne* and *M. affine* as "a natural group of small burrowing forms (1.5-5 mm) of slender build, and with uropod 3 linear in shape". *M. affine* is somewhat intermediate between *Corophium* sens. str. and *Medicorophium*, n. g., but is here included within the latter (Fig. 38, phenogram). Members of the genus *Medicorophium* overlap distributionally in northwestern Europe with *Corophium* sens. str., and with *Chelicorophium*, n. g., in the

KEY TO SPECIES OF *MEDICOROPHIUM*, NEW GENUS

1. Gnathopod 1 normally subchelate, palm distinct, little exceeded by dactyl . . . . . 2.
—Gnathopod 1 simple or weakly subchelate, palm short, greatly exceeded by dactyl . . . . . 5.

2. Antenna 2 subsimilar in both sexes, peduncular segment 4 toothed posterodistally . . . . . 3.
—Antenna 2 sexually dissimilar, pediform in male only . . . . . 4.

3. Antenna 2, flagellum elongate (10+ segments); rostrum projecting, apex rounded; uropod 1, rami spinose on both margins . . . . . *M. rotundirostre* (Stephensen)
—Antenna 2, flagellum short (5-6 segments); rostrum recessed, apex subtruncate; uropod 1, rami spinose on lateral (outer) margins only . . . . . *M. annulatum* (Chevreux)

4. Antenna 2, peduncular segment 4 lacking posterodistal process; uropod 2, margins of rami smooth; head, frontal margin with low rounded rostrum . . . . . *M. minimum* (Schiecke)
—Antenna 2, peduncular segment 4 with bidentate posterodistal process; uropod 2, rami with lateral marginal spine(s); head, frontal margin broadly convex, lacking distinct rostrum. . . . *M. affine* (Bruzelius)

5. Antenna 2 (male), peduncular segment 4 thick, deep; peduncular segment 3 short; rostrum low, triangular, projecting little beyond head lobes; uropod 1, inner ramus spinose. . *M. runcicorne* (Delle Valle)
—Antenna 2 (male), peduncular segment 4 relatively slender; peduncular segment 3 elongate; rostrum acute, extending beyond frontal margin; uropod 1, inner ramus setose . . . . . *M. aculeatum* (Chevreux)

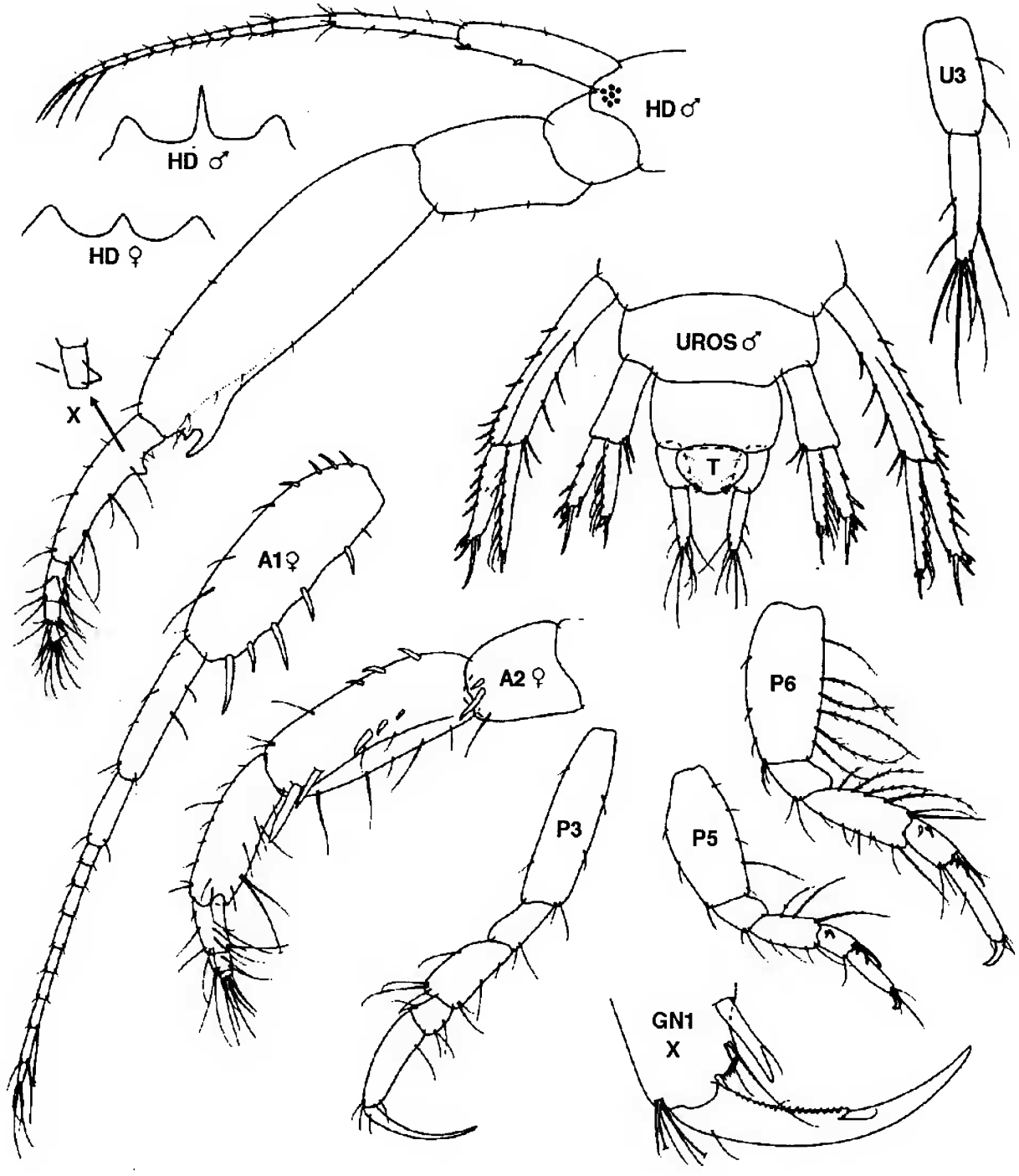

FIG. 8. ***Medicorophium aculeatum*** **(Chevreux). Mediterranean Sea. Male (3.0 mm); female (3.0 mm). (after Myers, 1982).**

eastern Mediterranean. However, in ordered character states of symplesiomorphic value, *Medicorophium* appears most closely similar to *Sinocorophium* (Fig. 38, phenogram). As noted elsewhere (p. 102), in the slender form of the urosome and uropods, lateral insertion of uropods 1 & 2, and the elongate apical spines of the uropod rami, among other character state similarities, *Medicorophium* may have given rise to an independent "cold-water" line of corophiins with fused urosome segments, conceivably ancestral to the genus *Crassicorophium.*

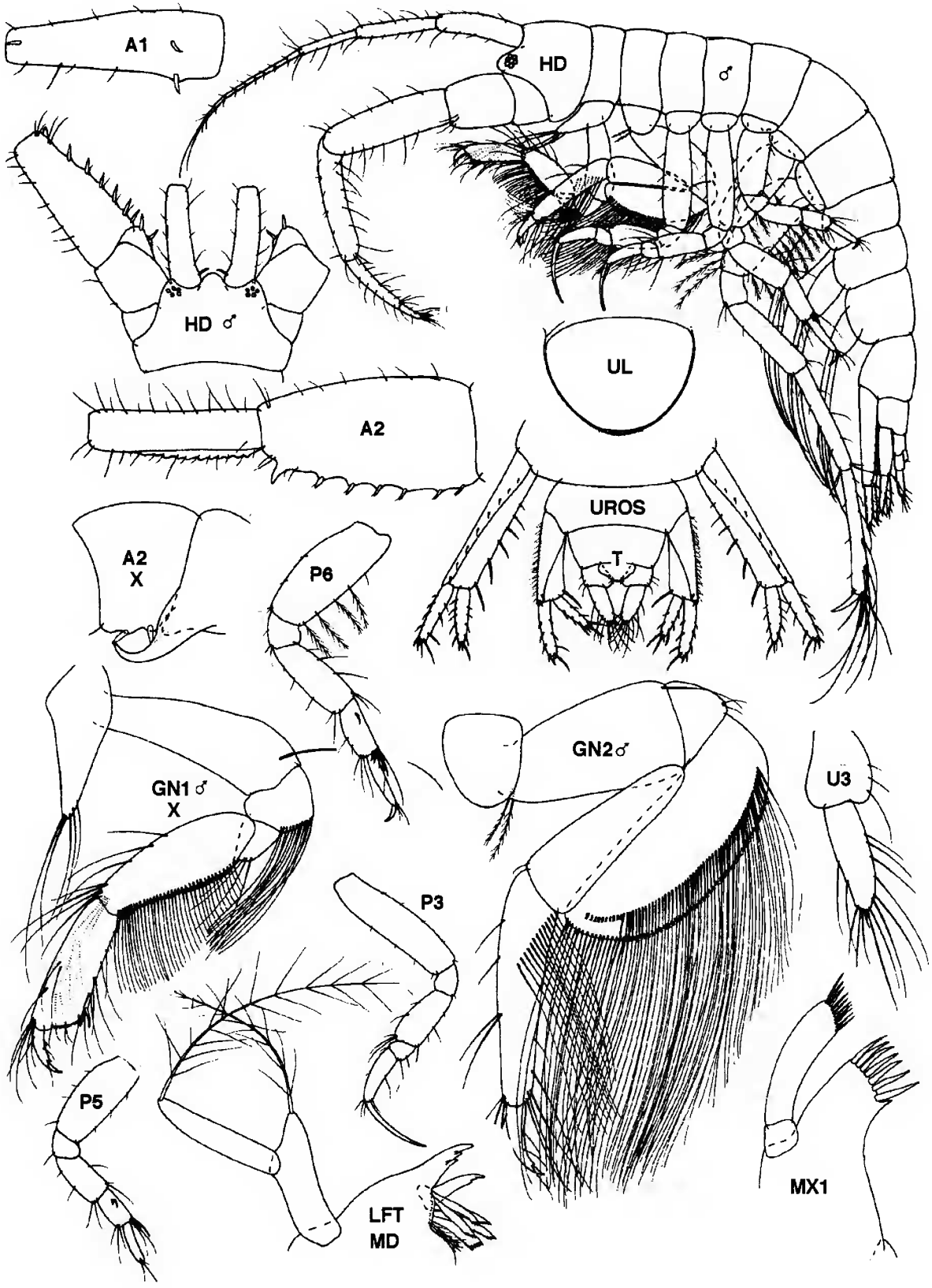

FIG. 9. ***Medicorophium rotundirostre*** **(Steph.). Mediterranean Sea. Male (6.0 mm); female (5.5 mm). (after Myers, 1982).**

Corophium Latreille
(See Figs. 10, 11)

Corophium Latreille, 1806: 58.—Stebbing, 1906: 685 (part).—Crawford, 1937: 595 (Section A, *volutator-arenarium* subgroup).—Gurjanova, 1951: 974 (part).—Bousfield, 1973: 198 (part).—Lincoln, 1979: 522 (part).—Myers, 1982: 185 (part).– Barnard & Karaman, 1991: 184 (part).

Type species: *Oniscus volutator* Pallas, 1766 (North Sea & English Channel).

Species. *Corophium multisetosum* Stock, 1952; *C. arenarium* Crawford, 1937; *C. orientale* Schellenberg, 1928.

Diagnosis. A relatively primitive complex of species, but more advanced than western North Pacific counterparts. Urosome segments not coalesced. Head, rostrum usually distinct; inferior antennal sinus recessed. Antenna 1 elongate, peduncular segment 3 medium. Antenna 2 large, pediform in male, less strong and often lacking process in female; segment 4 with single-toothed posterodistal process; segment 5 lacking median tooth and distal process; flagellum shorter than peduncle 5, proximal segment elongate; gland cone medium, not conspicuous.

Mouthparts plesiomorphic: Upper lip, epistome little produced. Lower lip, mandibular lobes short. Mandibular palp basic (type P1 of Hirayama, 1987b). Maxilla 1, palp slightly broadened distally, longer than outer plate. Maxilliped, inner plate medium, subacute; outer plate large, inner margin strongly setose; palp segment 2 elongate.

Gnathopod 1, propod regular, palm vertical; dactyl short, simple. Gnathopod 2 not greatly larger; propod slender; dactyl medium, simple, lacking posterior marginal teeth.

Peraeopods 3 & 4, basis slightly broadened; segment 4 little broadened distally; segment 5 medium short; dactyls medium. Peraeopods 5 & 6 basis setose behind; segment 4 long, broadened anterodistally; segment 5 shortened, posterodistal hook spines elongate, segment 6 and dactyl reversed. Peraeopod 7 elongate; basis, margins strongly setose; segment 4 shortened; dactyl short.

Pleon plate 3, hind corner obtuse or rounded. Pleopod peduncles broader than deep. Uropods 1 & 2, peduncles medium; rami straight, outer margins spinose; apices rounded. Uropod 3, ramus short, longer but less broad than peduncle. Telson broadly subtriangular, with few dorsal hook spines.

Coxal gills medium, sac-like, on peraeopods 3-6. Brood lamellae short, slender with relatively few (<20) marginal setae.

Distributional ecology: These medium to relatively large species burrow directly into muddy or sandy substrata where they construct sediment-lined U-shaped abodes. Species are endemic to the northeastern Atlantic and Mediterranean regions where they overlap with the *Medicorophium* and *Chelicorophium* subgroups.

Taxonomic commentary. Most species conform closely to the diagnosis above. However, *Corophium affine* Bruz.. is unique in lacking a well-defined rostrum, and other distinct features. It appears closest to the *volutator* type, but connects slightly below the 75% similarity level with genus *Medicorophium* (*aculeatum* type) (see phenogram, p. 130). Its character states are a mixture of the two: head rounded, linear uropod 3; antenna 1 short segment 3; antenna 2 (male) segment 4 bi-toothed; uropods 1 & 2, rami straight, etc.

Note: All previous records of *Corophium volutator* (and subspecies) from the western North Pacific (e.g., Hiray-ama, 1984, 1986) are probably attributable to one or more species of *Sinocorophium.* (p. 75).

KEY TO NORTH ATLANTIC SPECIES OF *COROPHIUM* LATREILLE (sens str.)

1. Antenna 2 sexually subsimilar, large, pediform in both sexes ..... 2.
—Antenna 2 sexually dissimilar, pediform in male only ..... 3.

2. Antenna 1 (male), peduncular segment 1 crenulate along lower inner margin; antenna 2, posterodistal process short, main tooth projecting slightly beyond end of segment 4; uropod 3, lateral lobe of peduncle weakly developed ..... *Corophium volutator* (Pallas)

—Antenna 1 (male), lower medial margin of peduncular segment 1 strongly setose, not crenulated; antenna 2, segment 4, large tooth of posterodistal process extending more than half its length beyond end of segment 4; uropod 3, lateral peduncular process strongly developed ..... *C. multisetosum* Stock

3.Antenna 1 (male), peduncular segment 1 crenulate along lower inner margin; uropod 1, outer margin of peduncle spinose throughout; uropod 3, ramus weakly setose ..... *C. orientale* Schellenberg
—Antenna 1 (male), peduncular segment 1 not crenulate along lower medial margin; uropod 1, proximal portion of outer margin of peduncle setose, distal portion spinose; uropod 1, inner ramus proximally strongly broadened; uropod 3, ramus strongly setose (10+ setae) ..... *C. arenarium* Crawford

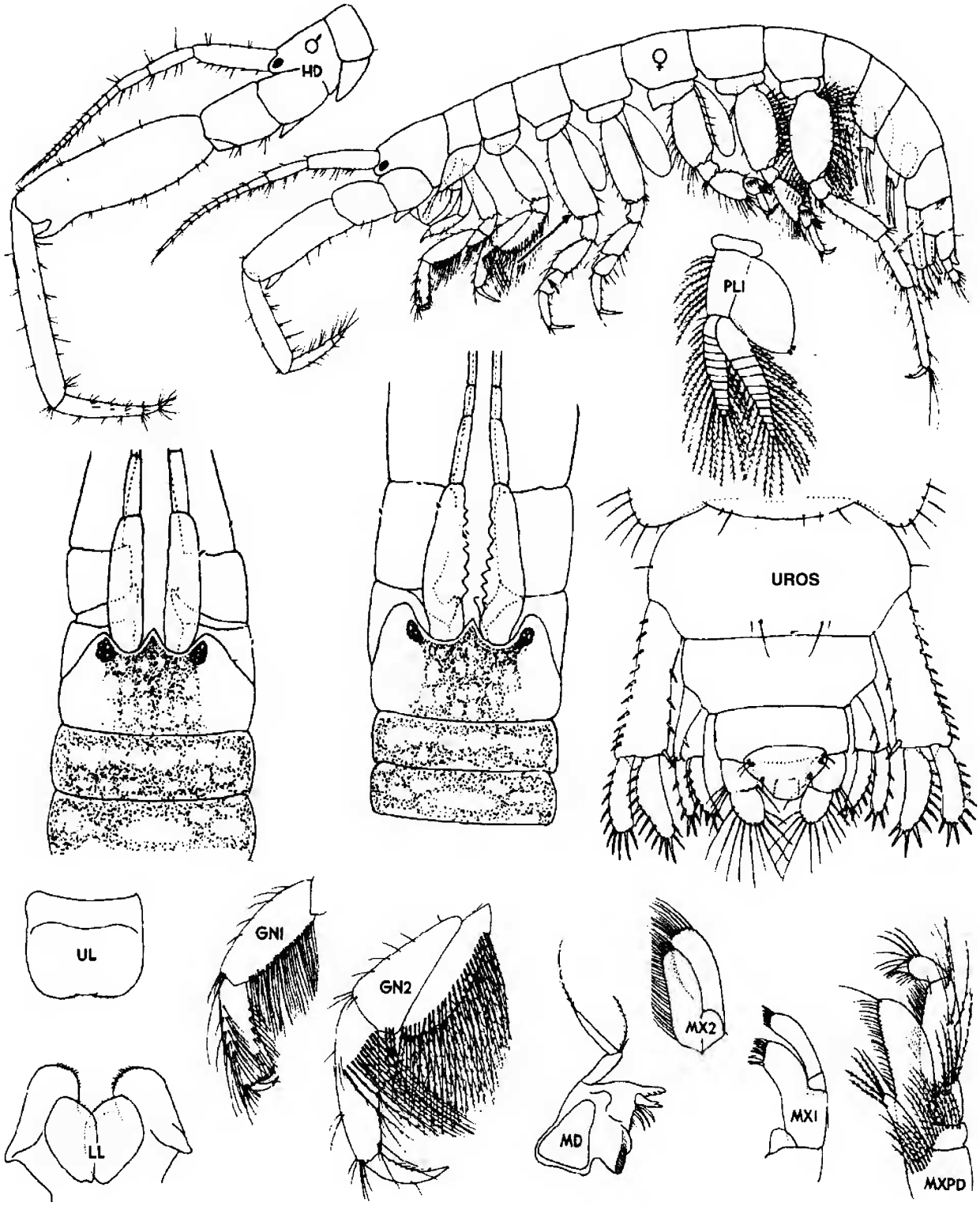

FIG. 10. ***Corophium volutator*** **(Pallas). Bay of Fundy. Male (6.0 mm); female 5.5 mm) (after Bousfield, 1973)**

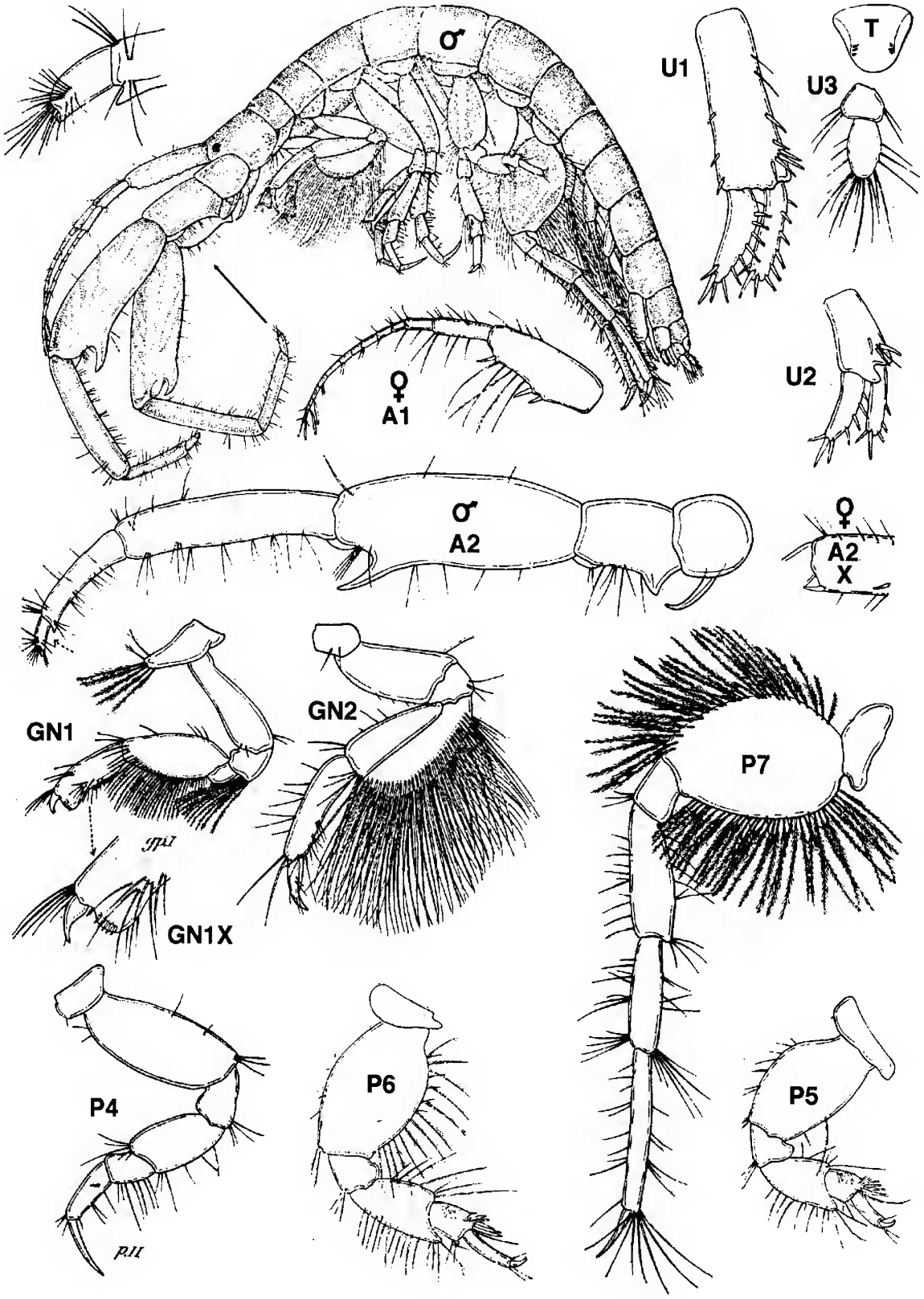

FIG. 11. ***Corophium orientale*** **(Schellenberg). Black Sea. Male (4.0 mm); female (to 7.5 mm) (after Carausu et al., 1955).**

Chelicorophium, new genus
(see Fig. 12)

Corophium Latreille, 1806, Stebbing, 1906: 685 (part).—Miloslawskaja, 1931: 61, Table, key).—Crawford, 1937: 594 (Section A, part).—Carausu et al., 1945: 359 (most).—Barnard & Karaman, 1991:185 (part).

Type species. *Corophium curvispinum* Sars, 1895b (present designation).

Species: *Chelicorophium chelicorne* Sars, 1895b; *C. robustum* Sars, 1895b; *C. maeoticum* Sowinsky,1898; *C. monodon* Sars, 1895b; *C. mucronatum* Sars, 1895b; *C. spinulosum* Sars, 1895b; *C. spongicolum* Welitchkovsky, 1914; *C. sowinsky* Martynov, 1924 ; *C. villosus* Carausu 1943; *C. nobile* Sars, 1895b; (?)*C. madrasensis* Nayar, 1950.

Diagnosis. Urosome segments not coalesced. Head, rostrum short, not exceeding anterior head lobes; inferior antennal sinus deeply regressed. Antenna 1 elongate, segment 3 medium. Antenna 2 strongly pediform and well developed (clasping) in both sexes; peduncular segment 4 with strong bidentate posterodistal process; segment 5 short, usually with median tooth near mid-point, distal process various; flagellum medium, ~ segment 5; gland cone short, inconspicuous.

Mouthparts variably plesiomorphic. Upper lip, epistome produced. Lower lip, mandibular lobes medium. Mandibular palp basic (type P1 of Hirayama, 1987b). Maxilla 1, palp sublinear, longer than outer plate. Maxilliped, inner plate short, apex subacute, inner margin with basal spine; outer plate regular, inner margin strongly setose; palp segment 2 medium to long.

Gnathopod 1, regularly subchelate; dactyl short. Gnathopod 2, propod slender, not longer than combined merus and carpus; dactyl short, typically tridentate.

Peraeopods 3 & 4, basis broad (glandular); segment 5 medium to short, not overhung by segment 4; dactyl short-medium. Peraeopods 5 & 6 short, basis setose behind; segment 4 short, lacking anterior lobe; segment 5 short, posterior hook spines strong; segment 6 and dactyl reversed (usually?). Peraeopod 7, basis strongly setose; segment 5 not elongate; dactyl short.

Pleon plate 3, hind corner rounded. Pleopod peduncles wide, broader than deep. Uropods 1 & 2 medium, peduncles broadening distally; rami short, straight; inner (as well as outer) margins often spinose or setose, apex little out-curved. Uropod 3, ramus longer than peduncle, slightly broadened, setose apically.

Telson short, broad, spinose hooks at hind corners and dorsally. Coxal gills medium broad, sac-like, on peraeopods 3-6. Brood lamellae short, sublinear, marginal setae not elongate.

Etymology. A combing form of the Greek prefix "cheli" - claw, and the generic root *Corophium*, with reference to the strongly pincer-like form of peduncular segments 4 & 5 of antenna 2.

Distributional ecology. Component species are endemic to the Aralo-Caspian region, confined mainly to the Black and/or Caspian Sea Basins, with a few outliers in the Mediterranean to the west, and Aral Sea to the east (formerly). Animals construct sediment-lined abodes in the shallow substratum, in salt, brackish, and tidal fresh waters.

Taxonomic commentary. Crawford (loc. cit.) included all species of this genus, except *C. villosus,* within section I of *Corophium* sens. lat. (segments of the urosome separate). He placed them phyletically between the *volutator-arenarium*, and the *salmonis-spinicorne* subgroups, the rationale for which is generally confirmed in the present study.

KEY TO BLACK SEA SPECIES OF *CHELICOROPHIUM*

1. Antenna 2, peduncular segment 5 lacking median tooth and distal process; peraeopods 3 & 4, segment 5 of medium length, distinctly longer than broad ..... *C. nobile* (G. O. Sars)
—Antenna 2, peduncular segment 5 with conspicuous median tooth and distal process; peraeopods 3 & 4, segment 4 short, not longer than broad ..... 2.

2. Gnathopod 2, dactyl bidentate posteriorly; uropod 2, inner ramus fully spinose .. *C. chelicorne* (G. O. Sars)
—Gnathopod 2, dactyl with 3-4 posterior marginal spines; uropod 2, inner ramus, inner margin bare ... 3.

3. Peraeopods 3 & 4, basis setose posteriorly; uropod 1 peduncle, outer margin setose .. *C. robustum* (Sars)
—Peraeopods 3 & 4, basis nearly bare posteriorly; uropod 1, outer margin of peduncle spinose ..... 4.

4. Antenna 2, segment 4 thickly and deeply incrassate, length <2Xwidth; uropod 1, outer margin of peduncle weakly spinose (4+); uropod 1, inner ramus spinose on outer margin only..... *C. maeoticum* (Sowinski)
—Antenna 2, segment 4 moderately stout, length > 2X width; uropod 1, outer margin of peduncle strongly spinose (10+); uropod 1, inner ramus spinose on both margins ..... *C. curvispinum* (G. O. Sars)

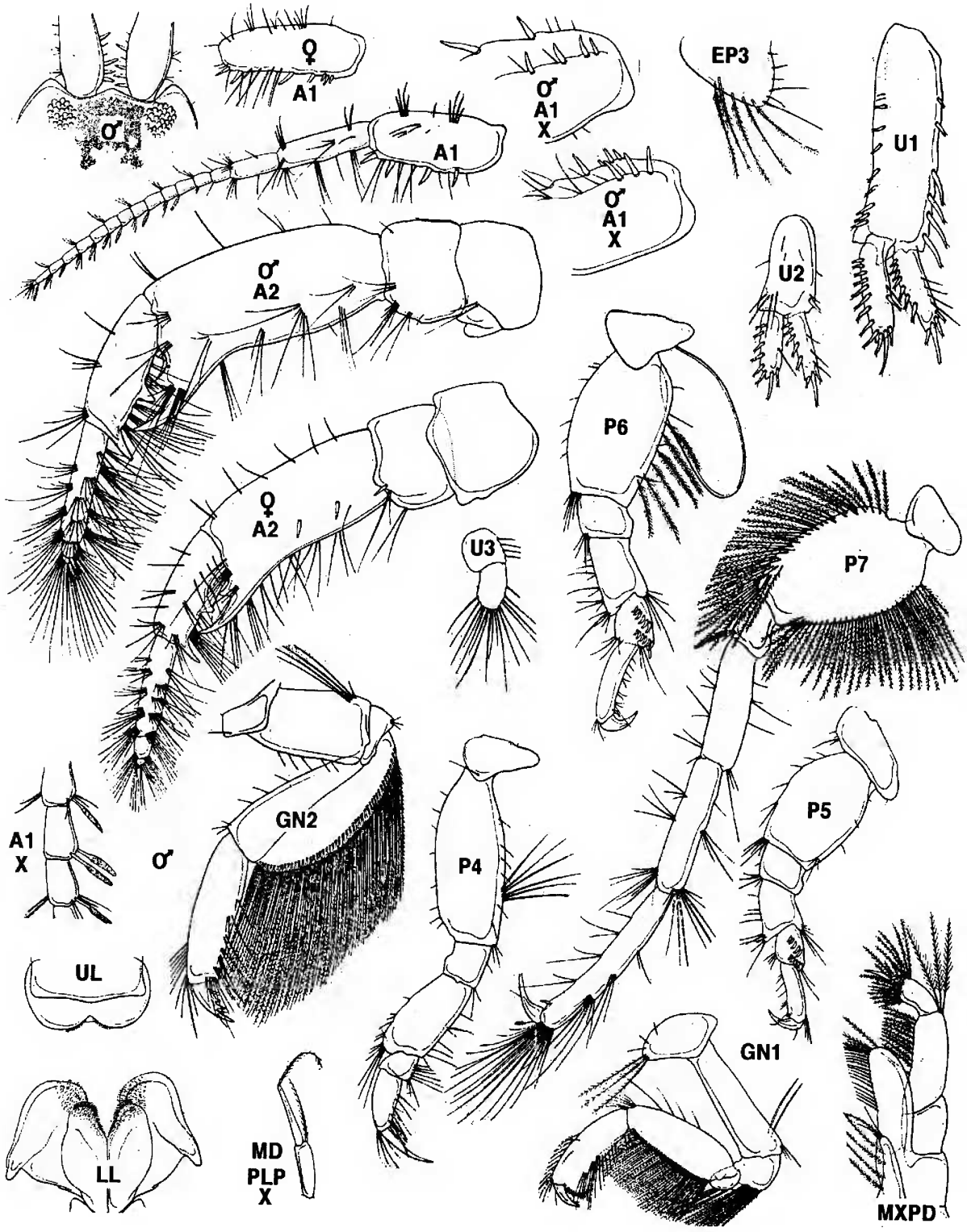

FIG. 12. ***Chelicorophium chelicorne*** **(G. O. Sars). Black Sea. Male (8.0 mm); female (7.5 mm) (after Carausu et al., 1955).**

Americorophium, new genus

Corophium Lateille, 1806, Stebbing, 1906: 685 (part).—Crawford, 1937 (Section A, part).—Shoemaker, 1949: 66 (part + key).—Barnard, 1969a: 190 (part).—Barnard, 1973: 17 (part).—Otte, 1976: 2 (part + key).—Barnard & Karaman, 1991: 184 (part).

Type species. *Corophium spinicorne* Stimpson 1857 (present designation).

Species. *Americorophium salmonis* (Stimpson, 1857); *A. brevis* (Shoemaker, 1949); *A. stimpsoni* (Shoemaker, 1941); 1949; *A. panamense* (Shoemaker, 1949); A. *setosum* (Shoemaker, 1949); *A. rioplatense* (Giambiagi, 1929); *A. aquafuscum* (Heard & Sikora, 1972); *A ellisi (*Shoemaker 1943)(?); *A. triaeonyx* (Stebbing, 1904)(?).

Diagnosis. Generally medium to large corophiins. Urosome segments unfused. Head, rostrum flat, rounded,or weakly produced; inferior antennal sinus large, regressed. Antenna 1, peduncular segment 3 variously shortened. Antenna 2, large, pediform, variously sexually dimorphic, often strongly setose posteriorly; gland cone short; segment 4 with bidentate posterodistal process; segment 5, posteromedian tooth and distal process variously developed; flagellum 2(3)-segmented, distal segments very short.

Lower lip, mandibular lobes pronounced. Mandibular palp basic (type P1 of Hirayama, 1987b). Maxilla 1, palp little (or not) exceeding outer plate. Maxilla 2, plates large, inner margins fully setose. Maxilliped, inner plate straight, setose apico-medially; outer plate regular, inner margin fully setose; palp segment 2 medium to short.

Gnathopod 1 regularly weakly subchelate; dactyl slightly exceeding palm. Gnathopod 2 strong; merus not occluding postero-distal free margin of carpus; dactyl moderately strong, spinose or toothed behind.

Peraeopods 3 & 4, bases broadened, glandular; segment 4 broadened distally, variously overhanging shortened segment 5. Peracopods 5 & 6, bases broadened, that of peraeopod6 setose behind; segment 5 shortened, with short posterodistal hook spines; segment 6 and dactyl reversed. Peraeopod 7; segment 5 not longer than 4; dactyl moderate.

Pleon plate 3, hind corner obtuse. Pleopod peduncles strongly broadened medially. Uropods 1 & 2 stout, peduncles broadened distally; outer ramus shorter than inner ramus; lateral margins of rami spinose, apices acute, curved outward. Uropod 3, ramus medium broad, slightly longer than peduncle. Telson broad,narrowing distally, apex subtruncate.

Brood plates large, strap-like, marginal setae long, numerous (>40). Coxal gills large, sac-like, on peraeopods 3-6.

Etymology. A combining form of the prefix "Ameri"- and the generic root *Corophium*, reflecting the essentially North American and neotropical distribution of known species comprising the genus.

Distributional commentary. Component species occur in North American Pacific boreal to warm-temperate and tropical coastal waters; also in North and South American Atlantic warm-temperate brackish estuaries. One species (*A. triaeonyx*) is endemic to the Indian Ocean.

Taxonomic commentary. Crawford (1937) linked *Corophium salmonis* Stimpson and *C. spinicorne* Stimpson and placed them between the Aralo-Caspian *C. chelicorne*, and the Mediterraean-endemic sublittoral *C. aculeatum* assemblages. He also linked *Corophium triaeonyx* Stebbing, redescribed fom Madagascar by Ledoyer (1982), most closely with *C. rioplatense* on the basis of similarities in antenna 2. These decisions find some supported here (Fig. 39, p. 132). In addition, the posterior margins of the peduncle and flagellum of antenna 2 are strongly setose in these Atlantic regional species of *Americorophium,* which include *A. aquafuscum* and *A. panamense. A. setosum* Shoemaker,1949, a small species with segmented urosome from the Pacific coast of Mexico, may be referable here but is excluded from the analysis because all character states of the male, and many critical features of the female, are unknown. In the medium-large sexually dimorphic Floridian species, *"Corophium" ellisi* Shoemaker, 1943, the urosome is unsegmented, but on the basis of most other character states it is assignable to the genus *Americorophium.* Its primitive features include a relatively shallow inferior antennal sinus, a 3-segmented mandibular palp (type P1), and the dactyl of gnathopod 2 that is posteriorly setose rather than toothed.

Americorophium spinicorne Stimpson
(Fig. 13)

Corophium spinicorne Stimpson, 1857: 514.—Bradley, 1908: 227, pls. 9, 10.—Shoemaker, 1949: 74, fig 6.—Aldrich, 1961: 21, fig 2.—Barnard, 1975: 340 (key), fig. 141.—Otte, 1976: 9, figs. 4, 5.—Austin, 1985: 615.—Staude, 1987: 349 (+ key).— Barnard & Karaman, 1991: 186.

Material Examined: About 85 lots comprising more than 300 specimens, from SE Alaska through B. C. to Washington, Oregon, and Central California, mostly in low-brackish estuaries, as follows:

ALASKA.

Southeastern Alaska. ELB Stns, 1961: A1 (21), A7(3), A9(3), A11(6), A27(26), A37(71), A74(1), A78(~50), A88(18), A153 (1), A159(10).

BRITISH COLUMBIA.

Queen Charlotte Islands. ELB Stns., 1957: H2a(2), H4 (67), H5(14), W6(6), W7a(1), H8(8), W9(6), W9b(11), W12b(2), H5(30), H15(1), E17-18(15), E25(4).

North-central mainland coast. ELB Stns, 1964: H4(1), H6(6), H7(1), H14(2), H18 (16), H46(2), H51(6), H54(12), H56(4), H57(5), H58(1).

Vancouver Island, north end and adjacent mainland. ELB

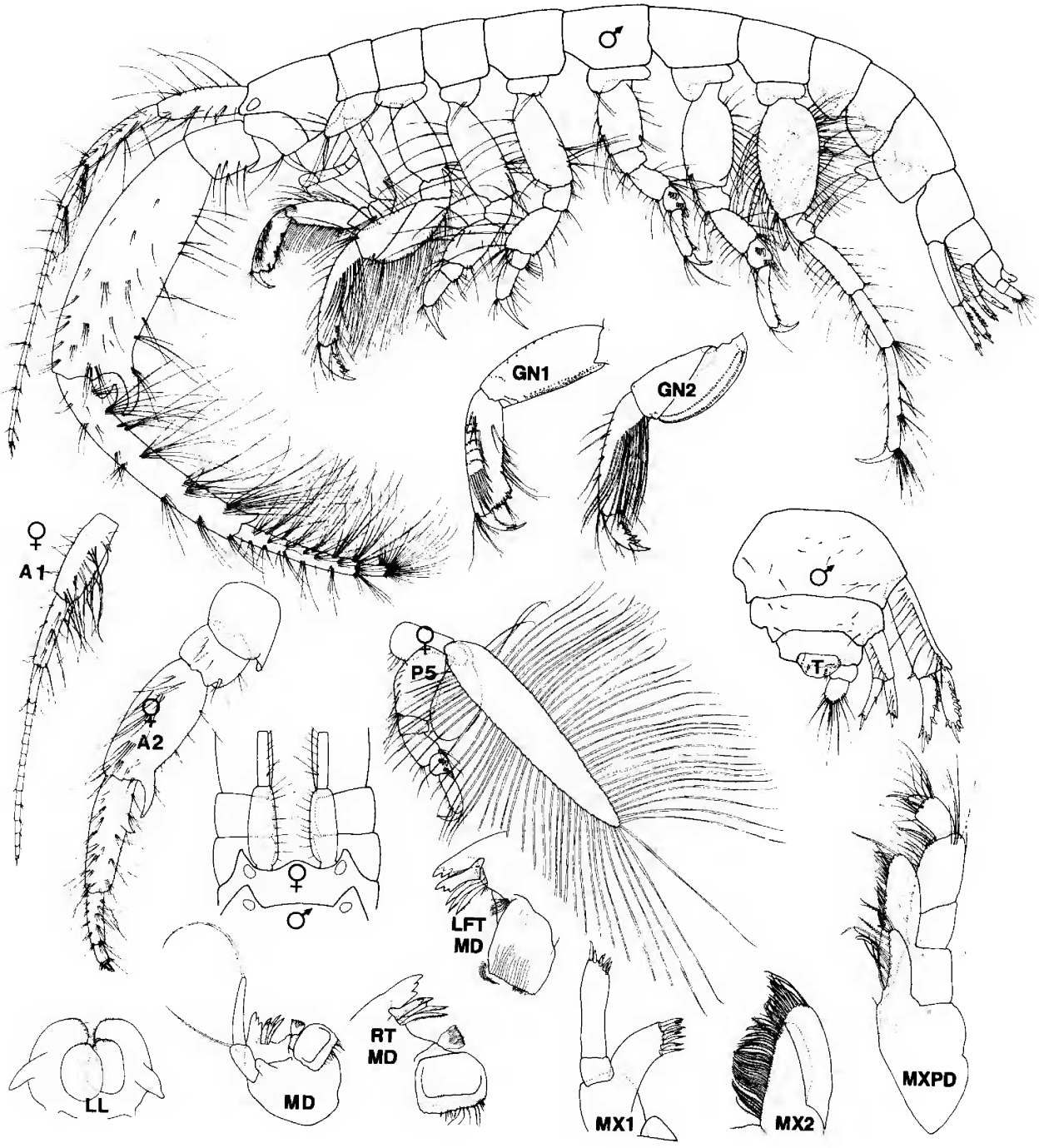

FIG. 13. ***Americorophium spinicorne*** **(Stimpson). Chinook, WA. Male (6.5 mm); female (7.0 mm).**

Stns, 1959: O1(1), O4(22), O7(13), O17(16), V13(4), V17(1), V21(several, damaged), N10(1), N11(22), N13(16), N15(12), N18(3), N21(8).

Southern Vancouver Island and adjacent mainland. ELB Stns, 1955: F3(17), F4(1), F9(29), G5(13), G11(25), G21(18), G22(2), P2(5), P5(20), P5b(2), P7(1), M3(16), M5(18). ELB Stn., 1964: H43(2). ELB Stn., 1970: P713(11). ELB Stns 1975: P6c(3); P16a(1), P19a(~200). F. Rafi coll., Campbell River estuary, 1984: B4(6).

WASHINGTON-OREGON

Washington. ELB Stns, 1966: W11(25); W12(1); W34 (20); W36(18); W44(1); W48 (Chinook) - 67 spms., incl. male (6.5 mm)(**fig'd**); female ov (7.0 mm) (**fig'd**), CMN Cat. No. NMCC1992-0798.

Oregon. ELB Stn W57 (Cape perpetua) - 7 spmns.

Diagnosis. Male (6.5 mm): Antenna 1, peduncular segment 1 regular, inner margin setose; flagellum 12-14

KEY TO SPECIES OF *AMERICOROPHIUM*

1. Antenna 2 (male), posterior margin of peduncular segment 4 sparsely setose, or setose distally only; uropod 2, rami with 2 (or more) outer marginal spines . . . . . 2.
—Antenna 2 (male), posterior margin of peduncular segment 4 lined throughout with clusters of long setae; uropod 2, rami with 0-1 outer marginal spines . . . . . 6.

2. Antenna 2, similar (large, pediform) in both sexes; posterior margin of segment 5 and flagellum strongly setose; uropod 1, outer margin of peduncle lined with setae. . . . . 3.
—Antenna 2 strongly sexually dimorphic, pediform in male only; posterior margin of segment 5 and flagellum weakly (or not) setose; uropod 1, outer margin of peduncle lined with short spines. . . . . 4.

3. Uropod 1, outer margin of outer rami with numerous (10+) close-set spines; mandibular palp 3-segmented; North American Atlantic . . . . . *A. aquafuscum* (Heard & Sikora)
—Uropod 1, outer margin of outer ramus with 6-7 short spines; mandibular palp 2-segmented; North American Pacific . . . . . *A. spinicorne* (Stimps.) (p. 90)

4. Urosome segments fused; gnathopod 2, posterior margin of dactyl lined with setae; mandibular palp 3-segmented; N. American Atlantic. . . . . *A. ellisi* (Shoemaker)
—Urosome segments separate; gnathopod 2, posterior margin of dactyl lined with 4-5 teeth or spines as well as setae; mandibular palp 2-segmented; North American Pacific . . . . . 5.

5. Antenna 1 (male), peduncular segment 1 expanded medially into broadly rounding lobe; gnathopod 2, propod with small posterodistal cusp . . . . . *A. salmonis* (Stimps.) (p. 94)
—Antenna 1 (male) peduncular segment 1 not expanded medially, but with small ventral hook-like process; gnathopod 2, propod lacking cusp . . . . . *A. stimpsoni* (Shoem.) (p. 94)

6. Gnathopod 2, posterior margin with 4-6 teeth; uropod 3, ramus short, as broad as long . . . . . *A. brevis* (Shoem.) (p. 95)
—Gnathopod 2, posterior margin with 2 teeth; uropod 3, ramus longer than broad . . . . . 7.

7. Antenna 2 (both sexes), segment 5 with strong curved distal process; uropod 1, outer margin lined with slender spines; uropod 3, ramus broadened . . . . . *A. setosum* (Shoem.)
—Antenna 2 (both sexes), segment 5 lacking distal process; uropod 1, outer margin with short spines; uropod 3, ramus slender, distinctly longer than wide . . . . . 8.

8. Antenna 2 (male), posterior margin of peduncular segment 3 strongly setose; antenna 2 (female), segment 4 not produced posterodistally; Indian Ocean . . . . . *A. triaeonyx* (Stebbing)
—Antenna 2 (male), posterior margin of peduncular segment 3 nearly bare; antenna 2 (female), segment 4 produced posterodistally; Neotropical . . . . . 9.

9. Antenna 2 (female), peduncular segment 4 produced distally as a large triangular spinose process; antenna 1, peduncular segment 1, dorsal margin strongly setose; uropod 1, inner ramus bare . . . . . *A. panamense* (Shoemaker)
—Antenna 2 (female) distal process of segment 4 short, weakly spined; antenna 1, peduncular segment 1, dorsal margin normal; uropod 1, inner ramus with outer marginal spine(s). . . *A. rioplatense* (Giambiagi)

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segmented. Antenna 2 large, pediform; segment 3 weakly setose posteriorly; segment 4 hind margin sparsely setose, posterodistal process appearing single-toothed; segment 5 not shorter than 4, posterior margin with strong proximal tooth, 4-5 clusters of long setae, and strong distal process; flagellum not shortened, 3(4)-segmented, hind margin with numerous long setae.

Gnathopod 1, dactyl with small posterior marginal tooth; tip exceeding oblique palm. Gnathopod 2, basis little broadened; carpus medium, with distinct posterodistal free margin; propod lacking distal cusp; dactyl with 4-5 posterior marginal teeth.

Peraeopods 1 & 2, basis and segment 4, anterior margins loosely lined with long setae; dactyls slender, slightly longer than segment 6. Peraeopod 5, basis, margins weakly setose. Peraeopod 7, basis medium broad, margins of distal segments moderately setose; dactyl medium.

Pleon plate 3, hind corner subquadrate. Uropod 1, outer

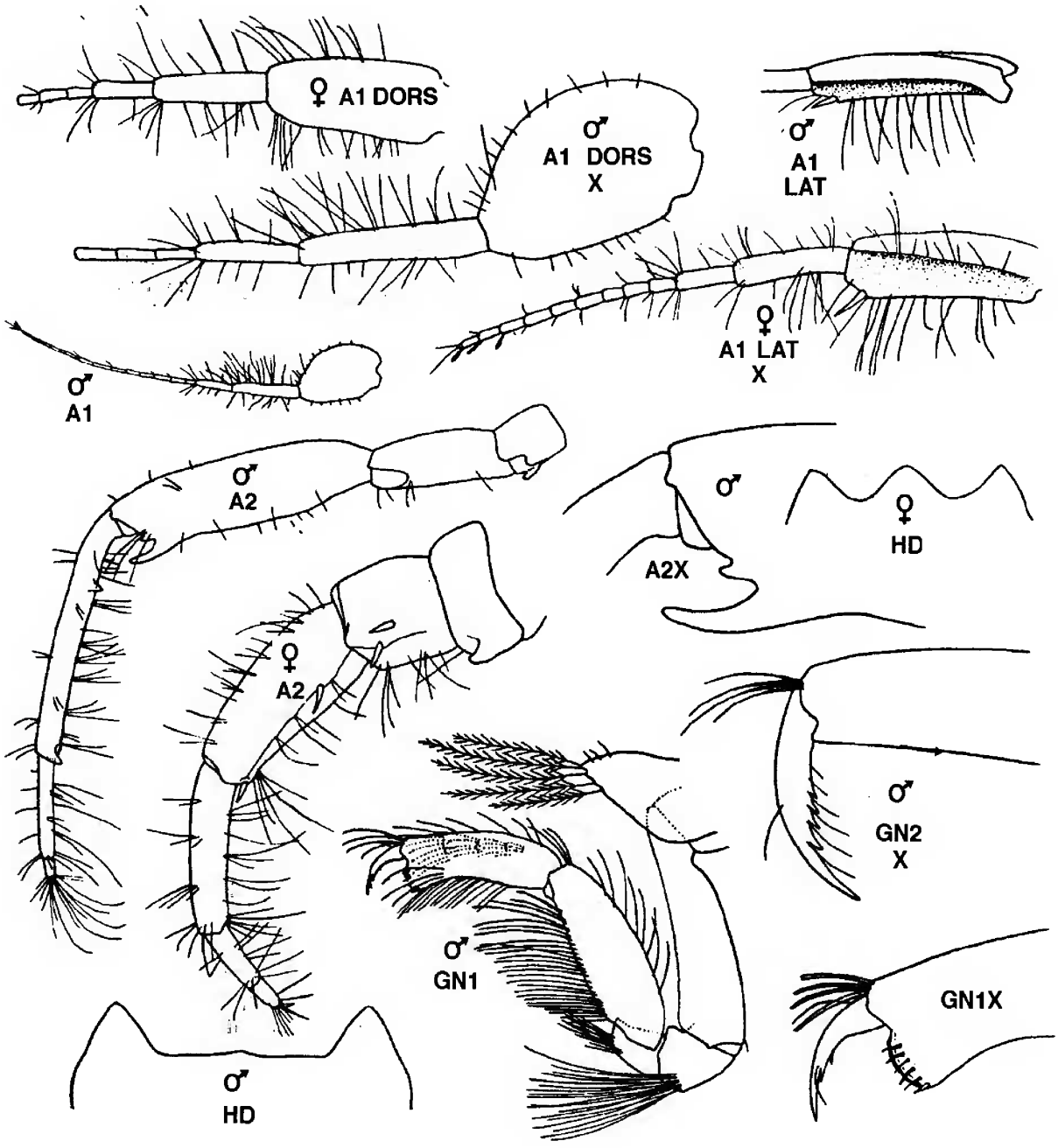

FIG. 14. ***Americorophium salmonis*** **(Stimpson). Puget Sound, WA. Male (6.0 mm); female (7.0 mm). (after Shoemaker, 1949).**

margin of peduncle lined with numerous setae of unequal length; rami unequal, outer margins with 5-6 spines. Uropod 2, rami unequal, outer ramus, outer margin setose; inner ramus, outer margin with 1-2 spines. Uropod 3, ramus and peduncle broadened, ramus nearly as wide as long. Telson wider than long, dorsally with 4 pairs of short hook spines.

Female (6.0 mm): Head, rostrum short, rounded. Antenna 2 similar in form (strongly pediform) but less robust than in male.

Brood plate large, strap-like, narrowing distally, margins lined with numerous (>60) long setae.

Taxonomic and distributional commentary. *Americorophium spinicorne* is the most commonly encountered estuarine corophiin amphipod of the northeastern Pacific region. The species occurs in a variety of intertidal habitats, but is most frequent in stream run-offs over shingle and mud flats, from the upper MW to LW levels.

Taxonomically, *A. spinicorne* exhibits mainly plesiomorphic character states, some in common with *A. aquafuscum* (Heard & Sikora) of American Atlantic warm-water estuaries (see Fig. 39, p. 132, and key, p. 92).

Americorophium salmonis (Stimpson)
(Figs. 14, 15)

Corophium salmonis Stimpson, 1857: 514.—Stebbing, 1906: 692.—Bradley, 1908: 235, pls. 11,12.—Shoemaker, 1949: 66, fig. 1.—Otte, 1976: 6 (key), figs. 4, 5.—Austin, 1985: 615.—Staude, 1987: 349 (key), 386, fig. 18.26.—Barnard & Karaman, 1991: 186.

Material Examined. About 250 specimens in 20 lots, mostly from high salinity outer coast locations, from Washington-Oregon north to the Queen Charlotte Islands; not recorded from SE Alaska.

BRITISH COLUMBIA.
Queen Charlotte Islands. ELB Stns, 1957: H5(5), H8a(35), H9(7), H10(4).
North-central mainland coast. ELB Stns, 1964: H13(1), H23(27).
Vancouver Island, north end. ELB Stns, 1959: O4(2), O12(10).
Vancouver Island, south end. ELB Stns, 1955: F3(5); F6(27), G11(3). ELB Stn., 1975: P20(3).

WASHINGTON.
San Juan Islands. ELB Stn, 1955: S5(1).
Washington, outer coast. ELB Stns, 1966: W15(7), W17(2), W29(2), W36(10), W40(1), W41(3), W48(13 spmns including male (6.0 mm)**(fig'd)**, female (7.0 mm) **(fig'd),** CMN Cat. No. NMCC1992-0798.

Diagnosis. Male (to 6.0 mm): Head, rostrum very short, little protruding beyond frontal margin. Antenna 1 peduncular segment 1 greatly broadened dorsomedially, inner margin weakly setose, flagellum slender, 12-14-segmented. Antenna 2 large, pediform; segment 3 elongate, posterior margin nearly bare; segment 4, surfaces and hind margin with scattered clusters of short setae, posterodistal process appearing single-toothed; segment 5 relatively slender, little shorter than 4, posterior margin with median proximal tooth, a few clusters of short setae, and medium-sized distal process; flagellum 3-segmented, ~1/2 length of segment 4, margins not strongly setose.

Coxa 1 with 5-6 antero-distal plumose setae. Gnathopod 1, dactyl with small posterior marginal tooth; tip exceeding rounded, nearly vertical palm. Gnathopod 2, basis little broadened; carpus medium, with distinct posterodistal free margin; propod with weak distal cusp; dactyl slender, with 4 small posterior marginal teeth and slender interdentate setae.

Peraeopods 1 & 2, basis, anterior margin loosely lined with longish setae; segment 4 broadened distally, partly overhanging short segment 5, anterodistal margin (of 4) richly long-setose; dactyl slender, curved, longer than segment 6. Peraeopod 5, basis setose anteriorly and posterodistally. Peraeopod 7 not unusually elongate, basis subovate; margins of distal segments moderately setose; dactyl medium, curved.

Pleon plate 3 shallow, hind corner tightly rounded. Uropod 1, outer margin of peduncle proximally with a few short setae, distally with short spines; rami strong, subequal, outer margins with 4-7 stout spines. Uropod 2 strong; rami subequal, outer margin with 2-3 spines. Uropod 3, ramus and peduncle little broadened, ramus distinctly longer than wide, margins setose. Telson very broad, short, hook spines short, indistinct.

Female (to 7.0 mm): Head, rostrum slightly stronger and more acute than in male. Antenna 1, peduncular segment 1 not strongly broadened, posterior margin with distal spine. Antenna 2 much shorter and strongly dissimilar in form to that of male; peduncular segments 4 & 5 short and stout, margins and surfaces with scattered short setae, but lacking stout spines; flagellum short, margins with short setae.

Brood plates broadly strap-like, margins lined with moderate numbers (~40) long setae.

Taxonomic and distributional commentary. *Americorophium salmonis* has been recorded subtidally from Puget Sound to the south coast of Alaska (Kodiak Island), on muddy bottoms in high salinity estuaries and fiords. It shows a mixture of character states, and clusters most closely with *A. stimpsoni* and other intermeiate species of the genus (see Fig. 39, p. 134).

Americorophium stimpsoni (Shoemaker)
(Fig. 16)

Corophium stimpsoni Shoemaker, 1941: 184.—Shoemaker, 1949: 68, fig. 2.—Barnard, 1975: 340 (key).—Barnard & Karaman, 1991: 186.

Material Examined: None in present collections.

Taxonomic and ecological commentary. This species ranges narrowly from San Francisco Bay north to Mendocino Bay, northern California, and possibly southern Oregon. The species was not listed by Otte (1975), Austin (1985), nor Staude (1987) from coastal waters of British Colombia or Puget Sound. It was not taken in at any of the present study sites in Washington and Oregon north to British Columbia. However, it is included in the key to species of *Americorophium* (p. 92) where it pairs closely with *A. salmonis* (Stimpson).

Americorophium stimpsoni shows several plesiomorphic character states, and clusters among the primitive to intermediate members of the genus (Fig. 39, p. 134). It was only partially described and figured by Shoemaker (1941, 1949). He found few reliable features for distinguishing females from those of *A. salmonis*. The males are readily distinguishable by: (1) the form of the rostrum which is much stronger, with apex rounded, in *A. stimpsoni*; (2) the form of peduncular segment 1 of antenna 1, that is not medially expanded but bears a ventral hook-like process in *A. stimpsoni*; and (3) by the form of antenna 2 in which segment 3 is shorter, the median tooth of segment 5 is more proximally positioned and the flagellum shorter than in *A. salmonis*.

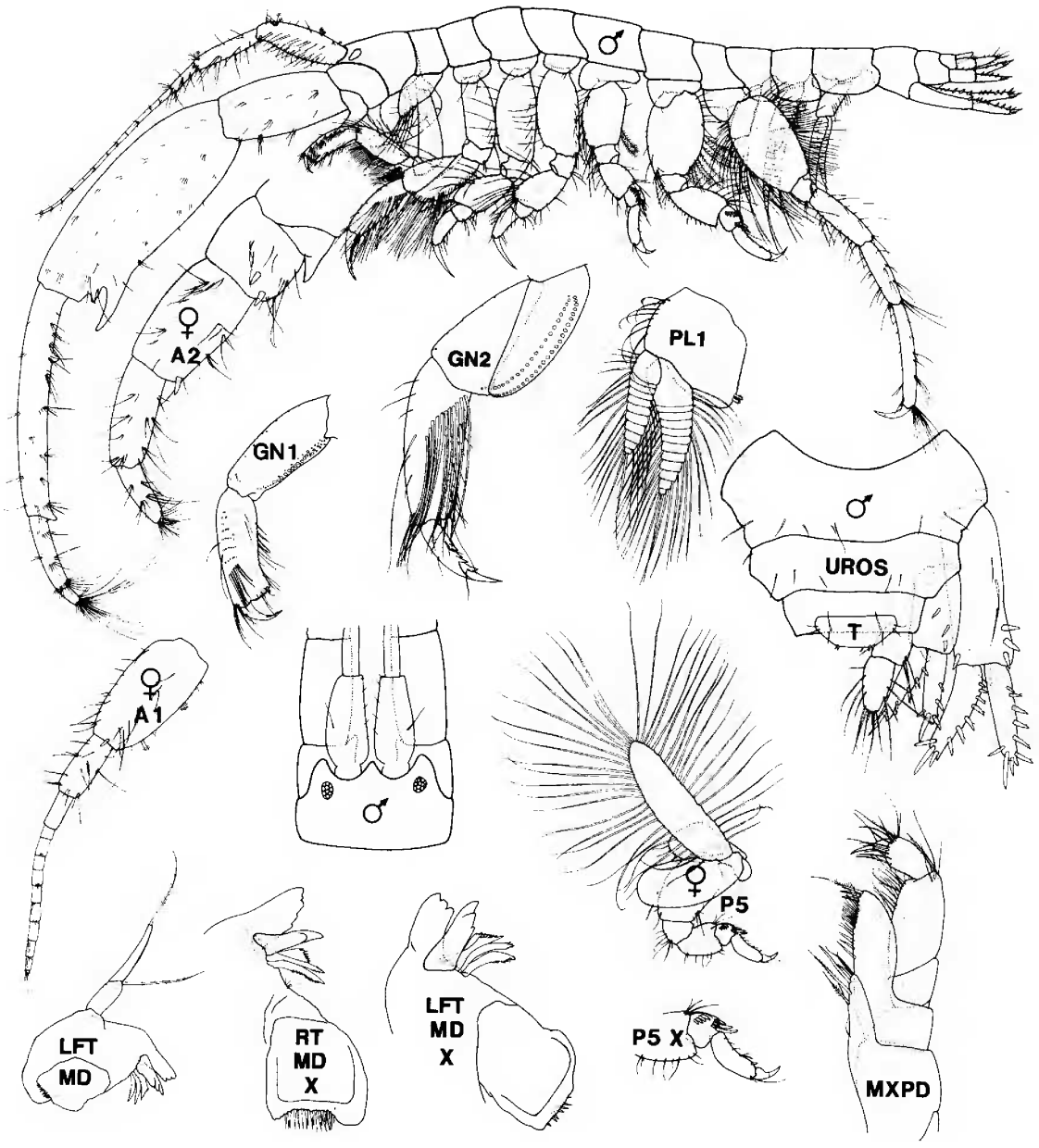

Fig. 15. ***Americorophium salmonis*** **(Shoem.). Chinook, WA. Male (6.0 mm); female (7.0 mm).**

Females of the two species do show slight overall difference in the antennae. In *A. stimpsoni*, the peduncular segments of antenna 1 are somewhat less strongly setose, and in antenna 2, peduncular segments 4 & 5 are relatively short and slender. However, despite the smaller overall size of *A. stimpsoni*, in gnathopod 1 the antero-distal setae of the coxa are more numerous, and the propod is less strongly broadened distally and the palm less strongly convex. In gnathopod 2, the dactyl is shorter and stouter, with fewer posterior marginal setae, than in *A. salmonis*.

Americorophium brevis (Shoemaker)
(Fig. 17)

Corophium brevis Shoemaker, 1949: 70, fig. 4.—Barnard, 1975: 340 (key), figs. 148, 149.—Otte, 1976: 6 (key), figs. 4, 5.—Coyle & Mueller, 1981: 9.—Austin, 1985: 615.—Staude, 1987: 349 (key), 386.—Barnard & Barnard, 1991: 185.

Material Examined. Nearly 200 specimens in 42 lots, mostly from interidal habitats of outer coast localities, from

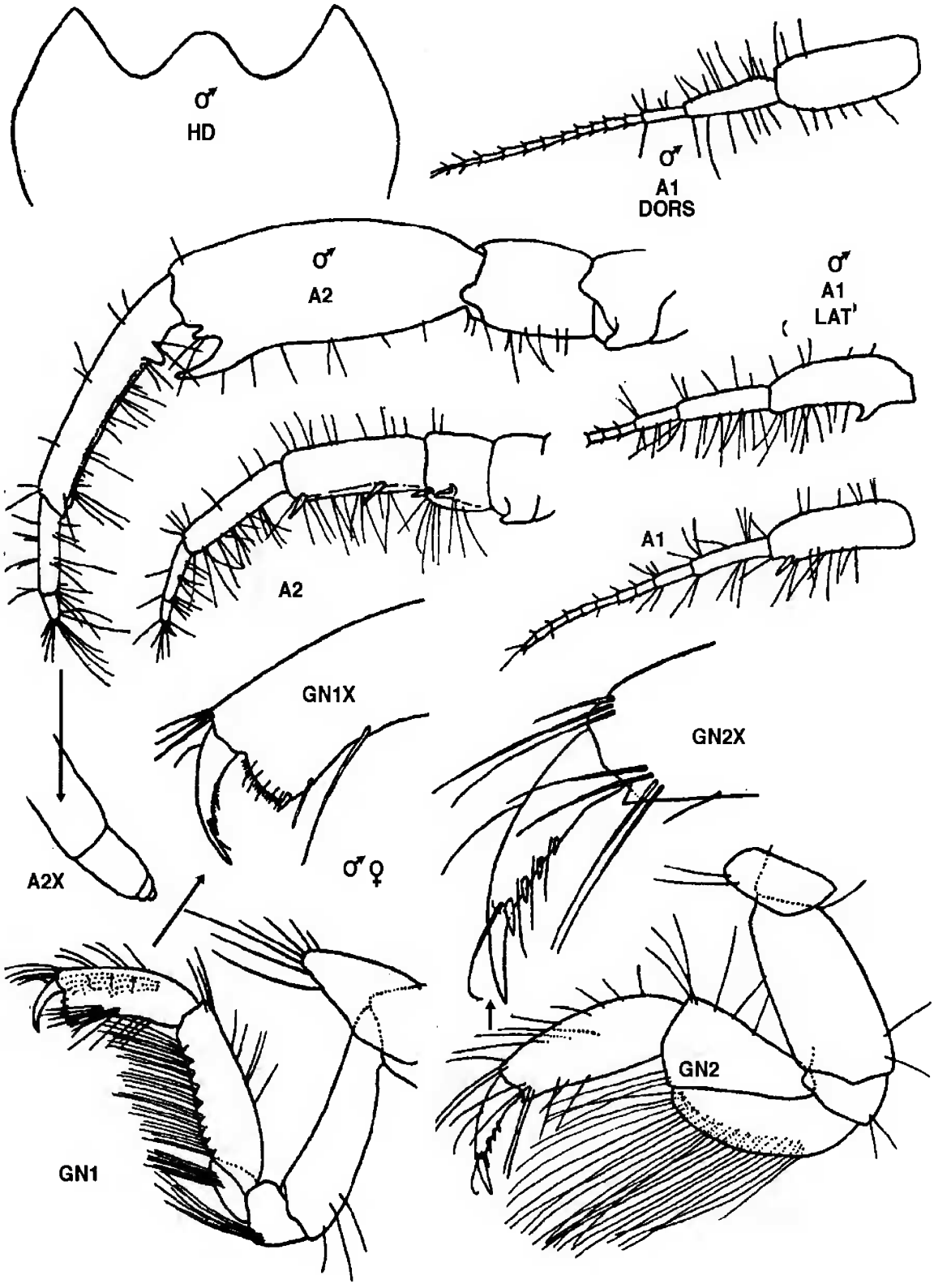

FIG. 16. ***Americorophium stimpsoni*** **(Shoemaker). Dillon Beach, CA. Male (5.0 mm); female (6.0 mm) (after Shoemaker, 1949).**

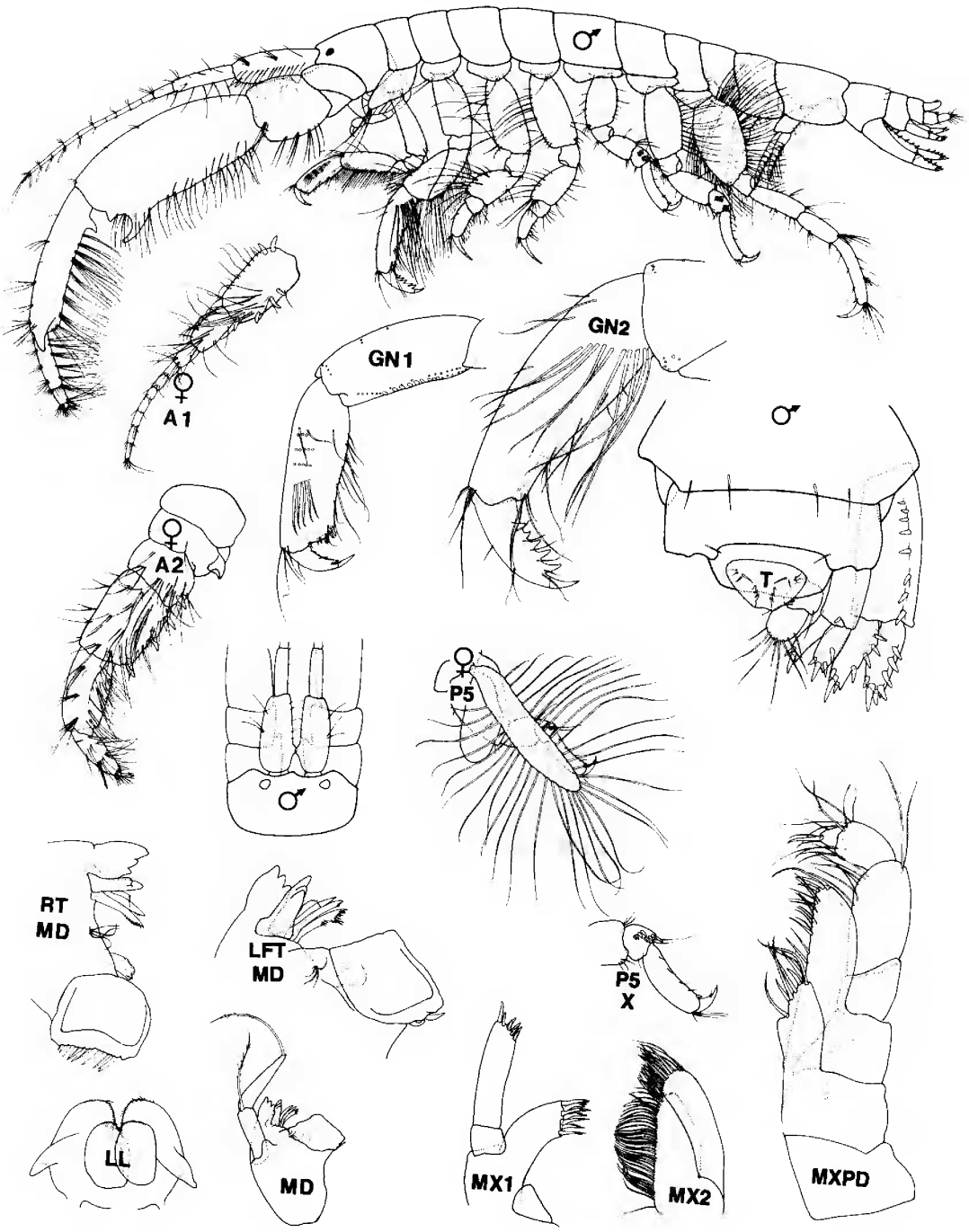

FIG. 17. ***Americorophium brevis*** **(Shoem.). Pacific Beach, WA. Male (3.5 mm); female (4.0 mm).**

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the Aleutian Islands, Prince William Sound and SE Alaska, through B. C. southward to Washington and Oregon: ALASKA.

Aleutian Islands. N.A. Powell coll., Thin Point, Unimak I., 1969 - 2 males, 2 females, 1 im.

Southeastern Alaska. ELB Stns, 1961: A43(4), A93(2), A99(1), A159(5). ELB Stns,1980: S5B3(1), S8B2(1), S13B1(4), S16B1(1).

BRITISH COLUMBIA.
Queen Charlotte Islands. ELB Stn, 1957: H14(1).
North-central mainland coast: ELB Stns, 1964: H8(1), H12(1), H16(3), H35(17), H39(3), H46(24), H58(2), H59(3), H61(7).
Vancouver Island, north end. ELB Stn, 1959: O13(2).
Vancouver Island, south end and mainland coast. ELB Stns, 1955: P2(4), P7(4), M8(2), M11(12). ELB Stns., 1964: H40(2), H41(2), H43(9). ELB Stn., 1970: P717(1). ELB Stn., 1976: B12(2).
Rocky Point, Wickaninnish Bay, C. Lobban Stn, 1972: CL1011(3); Cobble Beach, V.I. Stn., 1972: 335(1).

WASHINGTON-OREGON.
Washington, Point Roberts. ELB Stn, 1955: M10(23).
Washington, outer coast. ELB Stns, 1966: W2(1), W6(1), W20(14), W30(5), W34(2).
Oregon, outer coast, ELB Stn., 1966: W52(12).

Diagnosis. Male (5.0 mm): Head, rostrum very shallow, broad, not exceeding broad lateral head lobes. Antenna 1, peduncular segment 1 regular, inner margin with small proximal process, lateral margin setose; flagellum slender, 11-12 segmented. Antenna 2 large, pediform; segment 3 weakly setose posteriorly; segment 4 hind margin sparsely setose, posterodistal process appearing single-toothed; segment 5 not shorter than 4, posterior margin with strong proximal tooth, 4-5 clusters of long setae, and strong distal process; flagellum not shortened, 3-4 segmented, hind margin strongly long-setose.

Gnathopod 1, dactyl with minute posterior marginal tooth and fine proximal setae, tip exceeding oblique palm. Gnathopod 2, basis little broadened; carpus large, deep, with distinct posterodistal free margin; propod stout, narrowing distally, lacking distal cusp; dactyl with 5-6 unequal posterior marginal teeth.

Peraeopods 3 & 4, basis moderately broad, anterior margin moderately lined with long setae; segment 4 slightly overhanging short segment 5, anterodistal margin strongly setose; dactyl slender, length subequal to segment 6. Peraeopod 5, basis, margins weakly setose. Peraeopod 7 not elongate; basis medium broad; posterior margins of distal segments with clusters of longish setae; dactyl medium.

Pleon plate 3, lower margin smooth, hind corner rounded. Uropod 1, outer margin of peduncle lined with 7-8 short spines; rami short, unequal, outer margins with 4-5 spines. Uropod 2, rami subequal, outer margins with 1-2 spines. Uropod 3, ramus and peduncle broadened; ramus nearly as wide as long. Telson short, broad, dorsally with 4 pairs of short hook spines.

Female (4.0 mm): Head, rostrum little differing from male. Antenna 1, peduncular segment 1 with 2 proximomedian curved spines and 3-4 ventral marginal spines. Antenna 2 much shorter and strongly dissimilar in form to that of male. Peduncular segments 4 & 5 short, stout, facially and marginally setose; hind margin of segment 4 with 3-4 stout spines; flagellum short, margins setose.

Brood lamellae medium broad, strap-like, margins lined with medium numbers (35-40) of long setae.

Taxonomic and distributional commentary. *Americorophium brevis* was originally described from Puget Sound and recorded south to San Francisco Bay and north via Vancouver Island to southeastern Alaska (Shoemaker, 1949). The present study extends the range north to Prince William Sound, northern Gulf of Alaska.

Behaviourally, animals form U-shaped tubes in soft sediments, mainly subtidally to depths of ~35m. The species shows mainly apomorphic character states, and clusters most closely with the advanced *panamense-setosus* subgroup of Central American Pacific and Atlantic neotropical warm-water estuaries (Fig. 39, p. 132). It is least similar to the relatively primitive and more estuarine and intertidal species, *A. spinicorne*.

Microcorophium, new genus
(see Fig. 18)

Corophium Latreille, Hirayama, 1986: 451 (part + key).—Barnard & Karaman, 1991:184 (part).

Type species. *Corophium sextonae miospinulosum* Hirayama, 1986 (monotypy).

Diagnosis. Body minute. Urosome segments coalesced; uropods arising from lateral notches (Type F3 of Hirayama, 1987b). Head, rostrum medium to short, sexually dimorphic. Antenna 2 pediform in male (unlike and simple in female); segment 4 with bidentate posterodistal process; segment 5 lacking conspicuous median tooth or distal process; flagellum short, 3-segmented; gland cone pronounced.

Upper lip, epistome produced. Lower lip, mandibular lobes short. Mandibular palp of advanced form, with produced medial shelf (type P5 of Hirayama, 1987b). Maxilla 1, palp relatively short. Maxilliped, inner plate short, apex oblique; outer plate narrow, columnar, inner margin sparsely setose; palp segment 2 medium long, narrow.

Gnathopod 1, propod short, stout, palm strongly oblique; dactyl strong. Gnathopod 2, merus not occluding posterodistal (free) margin of carpus; propod with few proximomedial setae; dactyl medium strong, weakly bidentate.

Peraeopods 3 & 4, basis and segment 4 slightly broadened; segment 5 very short, partly overhung by segment 4. Peraeopods 5 & 6, segments 4 & 5 not shortened, posterolateral spines medium; segments 5 & 6 not reversed(?); dactyl short. Peraeopod 7, basis narrow; dactyl short.

Pleopod peduncles relatively narrow, little broader than deep. Pleon plate 3, hind corner weakly acute. Uropod 1, peduncle slender, weakly spinose; rami linear, apical spine elongate. Uropod 2 not reduced; rami linear, margins smooth, apical spine elongate. Uropod 3, ramus stouter and longer than peduncle. Uropod 3, ramus stout, longer than peduncle, weakly setose. Telson short, broad, rounded behind.

Coxal gills short, slender, sac-like, on peraeopods 2-6. Brood plates undescribed.

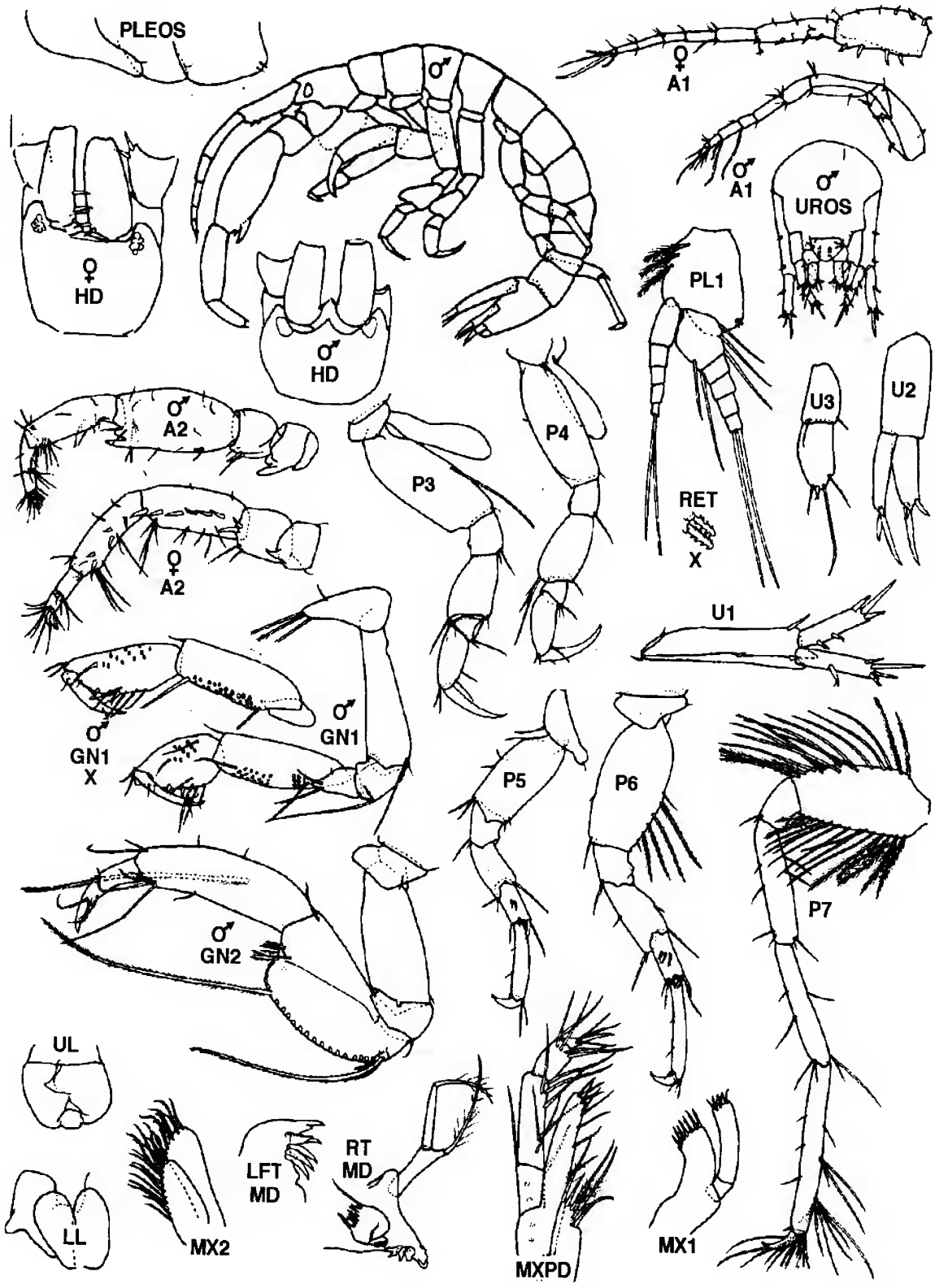

FIG. 18. ***Microcorophium miospinulosum*** **(Hirayama). Hong Kong. Male (1.4 mm); female (1.9 mm) (after Hirayama, 1986).**

Etymology: A combining form of the Greek prefix "micro", and the generic root *Corophium*., with reference to the minute size at maturity of the type species.

Distribution: Known only from the Hong Kong region of the South China Sea.

Taxonomic commentary. The type species *Microcorophium miospinulosum* was originally described as *Corophium sextonae* Crawford, 1937, subsp. *miospinulosum* Hirayama, 1986. The similarities noted by Hirayama between *miospinulosum* and *C. sextonae* would seem attributable to convergent morphology rather than close natural affinity. Thus, *C. sextonae* is a member of the genus *Monocorophium*, differing in several character states that are here considered of generic significance. In this species (as figured by Crawford, 1937 and Hurley, 1954) the epistome of the upper lip is not produced, the mandibular lobes of the lower lip are strong; the maxilliped inner plate is slender and subacute, the outer plate medium broad; gnathopod 1 is normally subchelate and the propod is slender; the dactyl of gnathopod 2 is short and tridentate; the pleopod peduncles are much broader; and in uropods 1 & 2 (male), the rami are short-spinose laterally and apically, and the apices are curved outwards and acute.

The specimens (4-5 mm) from Venice, Mediterranean Sea, figured by Myers (1982), as *Corophium sextonae* Crawford, 1937, differ somewhat in the bidentate (rather than tridentate) form of antenna 2, peduncular segment 4, and in the form and armature of the uropods.

In most character states *Microcorophium miospinulosum* must be considered a very primitive member of the corophiin subgroup having fused urosome segments. It may have evolved convergently from a *Sinocorophium*-like ancestor and is of distinctly different lineage than *Monocorophium,* sens. str. However, the form of the mandibular palp and gnathopod 1 may be considered autapomorphic within this unique genus.

Lobatocorophium, new genus
(see Fig. 19)

Corophium Latreille,1806, Hirayama, 1987a: 175 (part).—Ishimaru, 1994: 35 (part).

Type species. *Corophium lobatum* Hirayama, 1987a (monotypy).

Diagnosis. Small tube-building corophiins. Urosome segments fused; uropods arising laterally (type F3A of Hirayama, 1987b). Head, rostrum medium. Antenna 1, peduncular segment 3 short. Antenna 2 (female) ordinary, segments 4 & 5 little enlarged; flagellum 2-segmented. Antenna 2 (male) undescribed, but presumably large, pediform, segments 4 & 5 with pre-amplexing processes.

Upper lip, episome unproduced. Lower lip, mandibular lobes medium. Mandibular palp advanced (type P5 of Hirayama, 1987b). Maxilla 1, palp shorter than outer plate. Maxilla 2, lobes slender. Maxilliped, inner plate short, apex subacute; outer plate columnar, apex blunt, inner margin sparsely setose; palp segment 2 elongate, slender.

Gnathopod 2, palm of propod short, oblique, greatly exceeded by simple dactyl. Gnathopod 2, merus not occluding posterodistal (free) margin of short carpus;propod relatively short, with small posterodistal cusp; dactyl short, bidentate.

Peraeopods 3 & 4, basis broad, glandular; segment 4 broadened distally, overhanging short segment 5; dactyl long. Peraeopods 5, 6, and 7 not described.

Pleon 3 strongly rounded behind. Pleopod peduncles broader than deep. Uropod 1 appearing ventral to uropod 2; peduncle very slender rami short, linear, apical spines long. Uropod 2, peduncle large, outer margin strongly arched, setulose; rami short, inner ramus slender, apex subacute, outer ramus suboval, broader than long. Uropod 3, ramus broader and longer than peduncle, outer margin spinose.

Telson small, subtriangular, bare.

Coxal gills and brood lamellae not described.

Etymology. A combining form of the Latin prefix"lobatus" and the generic root *Corophium*, with reference to the lobate form of uropod 2.

Distributional ecology. Known only from shallow sandy substrata in the southeastern Sea of Japan.

Taxonomic commentary. In species of the genera *Apocorophium* (p. 123) and *Laticorophium* (p. 125), the lateral margins of the body that "plug" (occlude) the rear of the abode are formed mainly by the lateral margins of fused urosomal segments proper. The distal margin is formed by the short outer margin of the peduncle of uropod 2, and the peduncle and ramus of uropod 3 (e.g., in *Apocorophium acutum* (Fig. 35). In *Lobatocorophium,* however, the lateral margin of the "plug" is formed entirely by the strongly arched outer margin of the peduncle of uropod 2; the distal margin is formed by the outer ramus of uropod 2, and the broad ramus of the uropod 3 pair. This unique functional morphological difference of uropod 2 provides the principal basis for separate recognition of the genus *Lobatocorphium*.

Lobatocorophium lobatum (Hirayama)
(Fig. 19)

Corophium lobatum Hirayama, 1986: 175, figs. 1-5.

Diagnosis. Female (2.3 mm): The specimen described and figured by Hirayama (loc. cit.) lacked antenna 2. The species is very probably conspicuously sexually dimorphic. However, no other material has been described, so male-female differences are yet unknown.

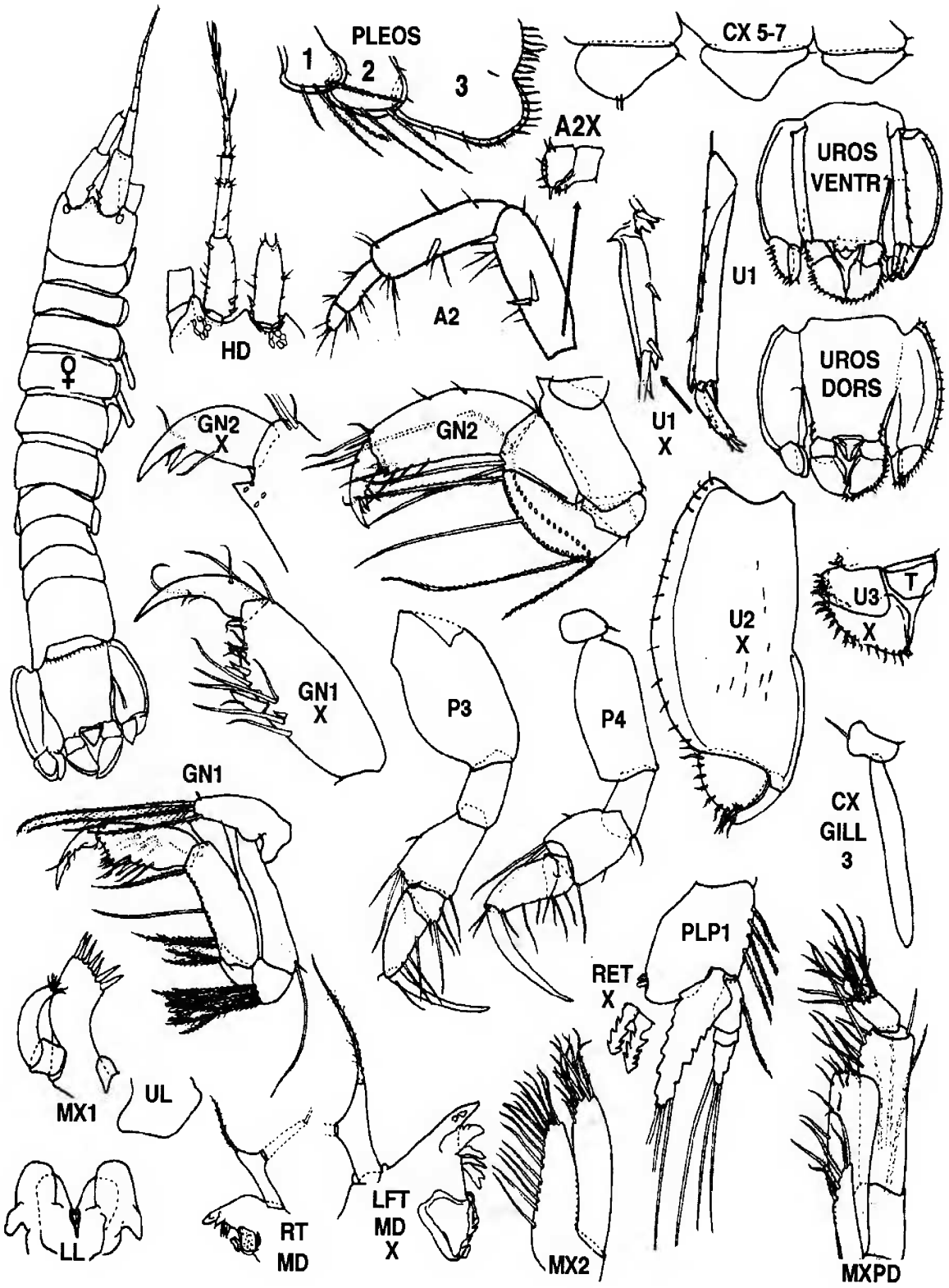

FIG. 19. ***Lobatocorophium lobatum*** **(Hirayama). Seto Inland Sea. Female (2.3 mm) (after Hirayama, 1987b).**

Crassicorophium, new genus

Corophium Latreille, 1806, Crawford, 1937: 606 (Section B, part).—Shoemaker, 1947: 47 (Section B + key, part).—Shoemaker, 1949: 66 (Section B + key, part).—Gurjanova, 1951: (part).—Just, 1970: 33 (part).—Bousfield, 1973: 198 (part).—Lincoln, 1979: 522 (part).—Hirayama, 1984: 2(+ key, part).—Barnard & Karaman, 1991: 184 (part).—Ishimaru, 1994: 35 (part).

Type species. *Corophium crassicorne* Bruzelius, 1859 (present designation).

Species. *Crassicorophium clarencense* (Shoemaker, 1949); *C. bonelli* (Milne Edwards, 1930).

Diagnosis. Urosome segments fused. Uropods 1 & 2 arising from distinct lateral notches. Head, rostrum short, acute, slightly sexually dimorphic; inferior antennal sinus strongly regressed. Antenna 1, peduncular segment 1 variously inflated and medially spinose (female); segment 3 short. Antenna 2 sexually dimorphic; gland cone medium; peduncular segment 4 (male), posterodistal process weakly bidentate, thickened and strongly spinose (female); segment 5 with weak median and distal processes; flagellum short, with apical spines.

Upper Lip, epistome produced. Lower lip, mandibular lobes weak to medium. Mandibular palp, proximal segment distally produced (type P5 of Hirayama, 1987b); spine row with several (4-5) slender blades Maxilla 1, palp slender, slightly exceeding outer plate. Maxilliped, inner plate with 4 strong setae; outer plate large; palp segment 2 medium.

Gnathopod 1, dactyl weakly bidentate, exceeding oblique palm. Gnathopod 2, merus fused with medium-long carpus except for short posterodistal portion; propod narrowing, with minute palm and posterodistal cusp; dactyl strong, weakly bidentate, finely crenulate behind.

Peraeopods 3 & 4 short; based broad, glandular; segment 4 moderately broadened distally, partly overhanging short segment 5; dactyls elongate. Peraeopods 5 & 6, medium; bases unequal in size, setose behind; segment 5 short, with 2 poster-olateral clusters of short hook spines; segment 6 and dactyls reversed. Peraeopod 7 moderately long; basis regular; segments 4 & 5 subequal in length; dactyl short.

Pleon plate 3, hind corner sharply rounded Pleopod peduncles narrow basally, broadened distally. Uropod 1, peduncle medium, outer margin proximally setose; rami subequal, nearly straight, apices acute, slightly (or not) curved outwards, one apical spine elongate. Uropod 2, rami straight, subequal, as long as peduncle. Uropod 3 little broadened; ramus medium, longer than unmodified peduncle. Telson short, wider than long, apex rounded.

Coxal gills slender sac-like, on peraeopods 3-6; brood plates elongate, strap-like, marginal setae numerous (30-40).

Etymology. Combining the Latin prefix "crassus" - thick, and the generic root *Corophium*, with reference to the very thick or incrassate antenna 2 of the female.

Distribution. Component species are holarctic in shallow shelf water, to depths of ~50 m.

Taxonomic commentary. The genus *Crassicorophium* is superficially similar overall to *Monocorophium*, but differs in character states of the mouthparts, gnathopods, and uropods that strongly suggest a separate immediate ancestry. Although not revealed by the phenogram (p. 130), primitive features of *Crassicorophium* (e.g., of urosome) suggest a natural affinity with *Medicorophium, Sinocorophium*, and the western Pacific complex of primitive genera rather than with the modern North Atlantic assemblage represented by *Americorophium* and *Monocorophium*..

Crassicorophium crassicorne (Bruzelius)
(Figs. 20, 21)

Corophium crassicorne Bruzelius, 1859: 15, fig. 2.—Sars, 1895a: 615, pl. 220.—Stebbing, 1906: 690, figs. 116-118.—Crawford, 1937: 607, figs. 4 a-f.—Shoemaker, 1947: 53, fig. 4.—Gurjanova, 1951: 976, fig. 679.—Bousfield, 1973: 201, pl . LXI.2.—Otte, 1976: 11, fig. 8.—Austin, 1985: 615.—Staude, 1987: 349 (key), 386.—Barnard & Karaman, 1991: 185.—Ishimaru, 1994: 35.

Material Examined. About 335 specimens in 23 lots, mostly in subtidal mixed sediments, from the Bering Sea and Aleutians Is. through SE Alaska, Queen Charlottes, and the north-central B. C. coast to the Strait of Georgia.

KEY TO SPECIES OF *CRASSICOROPHIUM*

1. Uropod 1, outer margin of peduncle spinose; uropod 2, margins of peduncle bare . . *C. bonelli* (p. 105)

—Uropod 1, outer margin of peduncle proximally setose; uropod 2, peduncular margins spinose . . . . . 2.

2. Antenna 2 (female), peduncular segment 4 very thick, incrassate, heavily spinose posteriorly; antenna 2 (male), segment 5 with distinct median tooth . . . . . *C. crassicorne* (p. 102)

—Antenna 2 (female), peduncular segment 4 normally stout and spinose; antenna 2 (male), segment 5, median tooth inconspicuous or lacking . . . . . *C. clarencense* (p. 105)

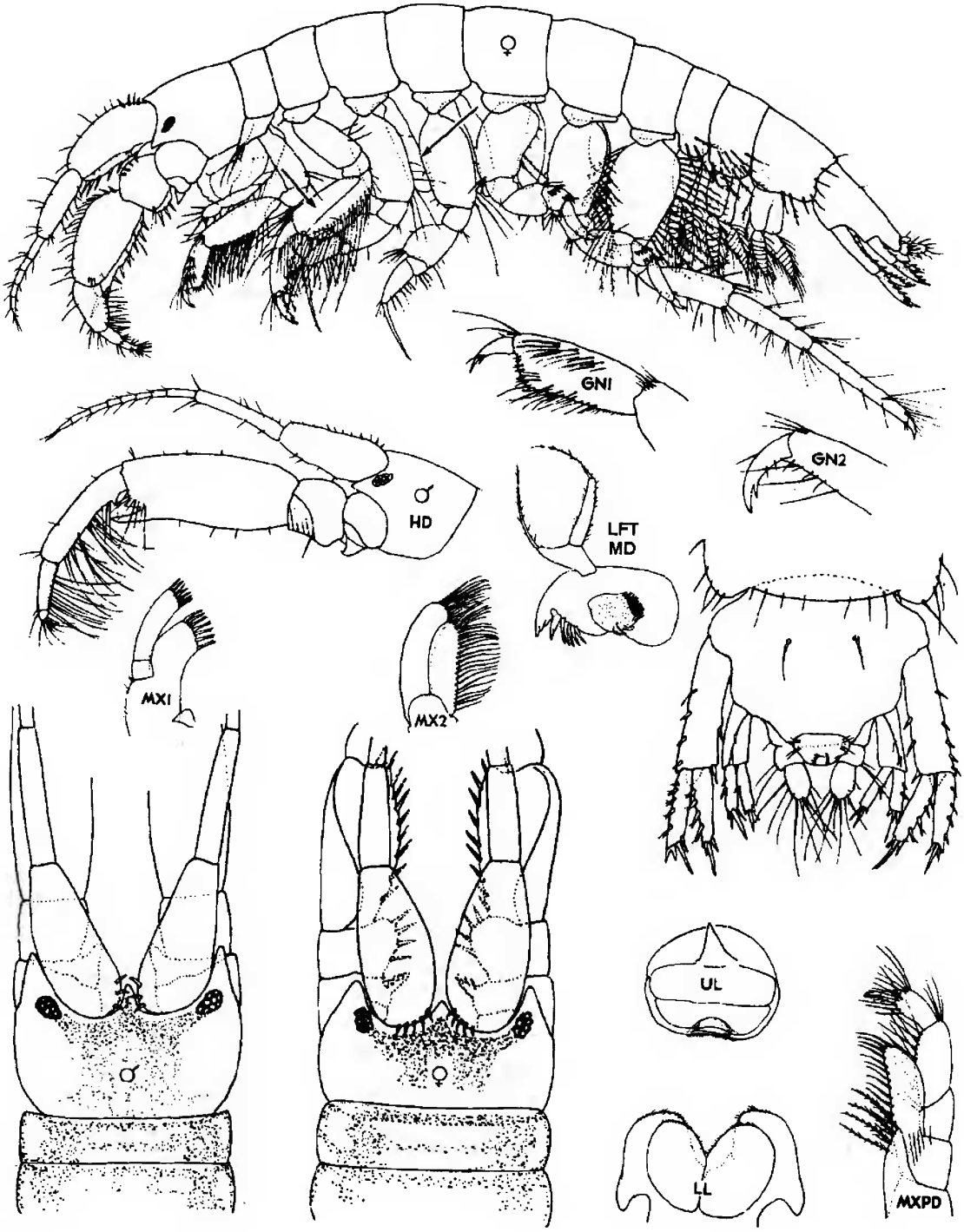

FIG. 20. ***Crassicorophium crassicorne*** **(Bruz.). Massachusetts Bay. Male (3.5 mm); female (3.5 mm) (after Bousfield, 1973).**

ALASKA.

Bering Sea Region. P. Slattery Stns, St. Lawrence I., 1980- 92 specimens.

Aleutian Islands. C.E.O'Clair Stns, St. Makarius Bay. 1969- 1972 - 7 specimens.

Unimak Island. N.A.Powell Stn., Izembek Lagoon., 1969 - 1 specimen.

BRITISH COLUMBIA.

Queen Charlotte Islands. ELB Stns, 1957: H3(14), H8b(12). North-central mainland coast. ELB Stn, 1964: H50(1). C. Levings Stns, Swanson Bay, 45-62 m, 1973: S1B,025-029(120). C. Levings Stns, 52-67 m, 1975: 002-012(66). Vancouver Island, north end. ELB Stn, 1959: V3 (Hope I.) - 9 spmns, incl. male (3.5 mm)(**fig'd**); female ov (4.0 mm) (**fig'd**), CMN Cat. No. NMCC1992-0735.

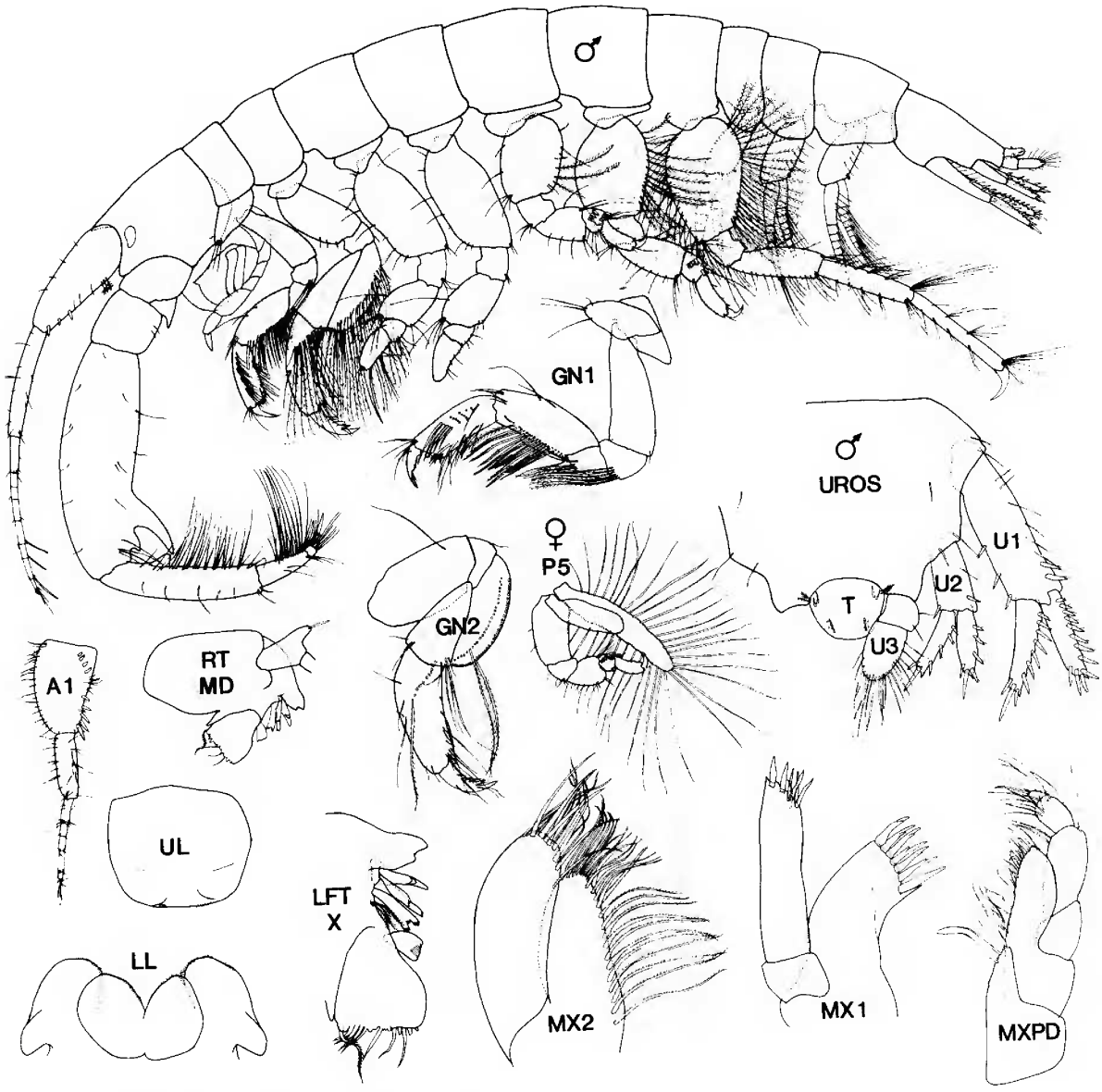

Fig. 21. ***Crassicorophium crassicorne*** **(Bruz.). Hope I., B. C. Male (3.5 mm); female (4.0 mm).**

Vancouver I., south end. ELB Stn, 1975: P5A(1). K. Conlan Stns, 1977. French Creek - 10 specimens; Saanich Inlet - 1 specimen.

Diagnosis. Male (3.5-4.0 mm): Pleosome segment 3 dorsally smooth. Urosome with distinct lateral notches; uropod 1 inserted entirely laterally. Head, rostrum short, recessed posterior to lateral head lobes. Antenna 1, peduncular segment 1 broadened proximally, with short proximal marginal spines; segment 2 slender; segment 3 short; flagellum slender, 7-8 segmented. Antenna 2 strongly pediform; peduncular segment 5 shorter than 4, with proximal median tooth and distal process, posterior margin strongly setose; flagellum 2(3)-segmented, posterior margin strongly setose.

Gnathopod 1, dactyl tip little exceeding oblique palm. Gnathopod 2, basis short, not broadened; carpus medium, with short posterodistal free margin; propod narrowing, with distinct posterodistal cusp; dactyl with single small posterior marginal tooth.

Peraeopods 3 & 4, bases broad, anterior margin weakly setose; segment 4 broad and overhanging small segment 5, anterior margin (of 4) nearly bare; dactyls large, nearly straight, longer than segment 6. Peraeopods 5 & 6, bases variously setose posteriorly. Peraeopod 7 medium; basis medium broad; distal segments marginally setose; dactyl short.

Uropod 1, peduncular outer margin distally spinose, proximally with a few setae; rami medium, each with 4-7 outer marginal spines. Uropod 2 medium; rami with 1-2 outer marginal spines, outer ramus shorter. Uropod 3, peduncle short, not broadened or lobate; ramus longer than broad, apical setae elongate. Telson short, broad, with 3 posterodorsal pairs of small hook spines.

Female (3.3-4.0 mm): Rostrum short, less strongly recessed than in male. Antenna 1, peduncular segment 1 strongly broadened, with 4-5 proximal marginal spines.. Antenna 2, peduncular segments 3 & 4 shorter, deeper, and more marginally spinose than in male, with strong flange-like posterodistal process; segment 5 very short, deep, posterior margin lined with medium setae; flagellum subequal in length to segment 5, distally with short setae.

Brood lamellae strong, strap-like, with numerous (35-40) long marginal setae.

Taxonomic commentary. Specimens from the North American Pacific region differ little from those of the North American Atlantic region. However, the material from Japanese and Korean coastal waters, identified as *Corophium crassicorne* by Hirayama (1984) and Kim (1991), respectively, shows several differences, especially in the antennae and gnathopods (Fig. 20, 21) from North Atlantic material and merit further comparison.

Distribsutional Ecology. A holarctic and subarctic species, extending southwards in the North Pacific to the Sea of Japan in the west, and British Columbia and Washington in the east; on sand and coarse sand, from LW level to depths of 37 m.

Crassicorophium clarencense (Shoemaker)
(Figs. 22)

Corophium clarencense Shoemaker, 1949: 78, fig. 7.—Just, 1970: 33, figs. 17-20.—Barnard & Karaman, 1991: 185.
Corophium bonelli (M-E) forma. Shoemaker, 1920: 22.

Material examined. One lot marginally from the study region. The holotype male specimen, and four female paratypes, from Port Clarence, Grantley Harbor, Alaska (northen Bering Sea), are in collections of the CMN, Ottawa.

Diagnosis. Male (4.0 mm): Pleosome segment 3 dorsally smooth. Urosome with distinct lateral notches; uropod 1 inserted entirely laterally. Head, rostrum medium, basally narrow, tip exceeding short lateral head lobes. Antenna 1, peduncular segment 1 broadened proximally, inner margin weakly setose; segments 2 & 3 relatively short; flagellum 6-7 segmented. Antenna 2 medium strongly pediform; peduncular segment 5 little shorter than 4, with very weak proximal median tooth and distal process, posterior margin with medium setae; flagellum very short, 3-segmented, posterior margin with longish setae.

Gnathopod 1, dactyl with weak posterior tooth, tip distinctly exceeding short palm. Gnathopod 2, basis short; carpus medium short, with short posterodistal free margin; propod with distinct posterodistal cusp; dactyl slender, with a single small posterior marginal tooth and a few setae.

Peraeopods 3 & 4 not described, probably much as in *C. crassicorne*. Peraeopod 5, basis little broadened, hind margin posterodistally setose. Peraeopod 7 not described.

Uropod 1, peduncular outer margin setose proximally, spinose distally; rami medium, subequal, each with 5-6 outer marginal spines. Uropod 2 medium; rami, outer margins each with 2-4 spines. Uropod 3, peduncle short, with small setose lateral lobe; ramus longer than broad, margins with long setae. Telson broader than long, apex rounded, with 4 posterodorsal pairs of small hook spines.

Female (3.8 mm). Rostrum short, very broad. Antenna 1, peduncular segment 1 with 2-3 proximo-median spines. Antenna 2 strongly dissimilar to male; peduncular segment 4 little broadened, posterior margin with 3-4 single spines and a few setae; segment 5 slightly shorter than 4, posterior margin with 3 pairs of strong spines; flagellum weakly setose posteriorly.

Brood lamellae relatively long, strap-like, with numerous (>40) marginal setae.

Taxonomic and distributional commentary. *Crassicorophium clarencense* is an intermediate member of the genus (Fig. 41, p. 133). Specimens from the western North American Arctic region (Shoem., loc. cit.) appear slightly more advanced than those from the eastern Arctic and Arctic-Atlantic region (Fig. 22), especially in characters of the antennae, gnathopods and uropods. Although *C. clarencense* was not taken strictly in the present study region, or previously recorded there (e.g., Otte, 1976), the species would not be unexpected along the western coast of Alaska, from the Bering Strait region perhaps southward to the glacial fiords of Prince William Sound.

Crassicorophium bonelli (Milne Edwards)
(Fig. 23)

Corophium bonelli Milne Edwards, 1830: 385.—Sars, 1895a: 616, pl. 221.1.—Crawford, 1937: 608, fig. 2,H-O.—Gurjanova, 1951: 978, fig. 681.—Bousfield, 1973: 202, pl. LXII.1.—Kudrjaschov, 1979: 127.—Myers, et al. 1989: 319, fig.1.—Barnard & Karaman, 1991:185.—Ishimaru, 1994: 35.
Corophium contractum Stimpson, 1856: 383 (material from Japan, possibly identical with *C. bonelli*, fide Stebbing, 1906).
non *Corophium bonelli* Shoemaker, 1920 [= *Crassicorophium clarencense* (Shoemaker, 1949)].

Material Examined. None from within the North Pacific study region.

Diagnosis. Female (4.5-6.0 mm): Pleosome segment 3 posterodorsally smooth. Urosome with distinct lateral notches; uropod 1 inserted mainly laterally. Head, rostrum short, apex level with inferior head lobes. Antenna 1, peduncular segment 1 broadened proximally, with 3 inner marginal spines; segments 2 & 3 relatively short; flagellum short, 5-6 segmented. Antenna 2, segments 3-5 normally stout; peduncular segment 4 with 3 posterior margin pairs of medium spines; segment 5 little shorter than 4, posterior

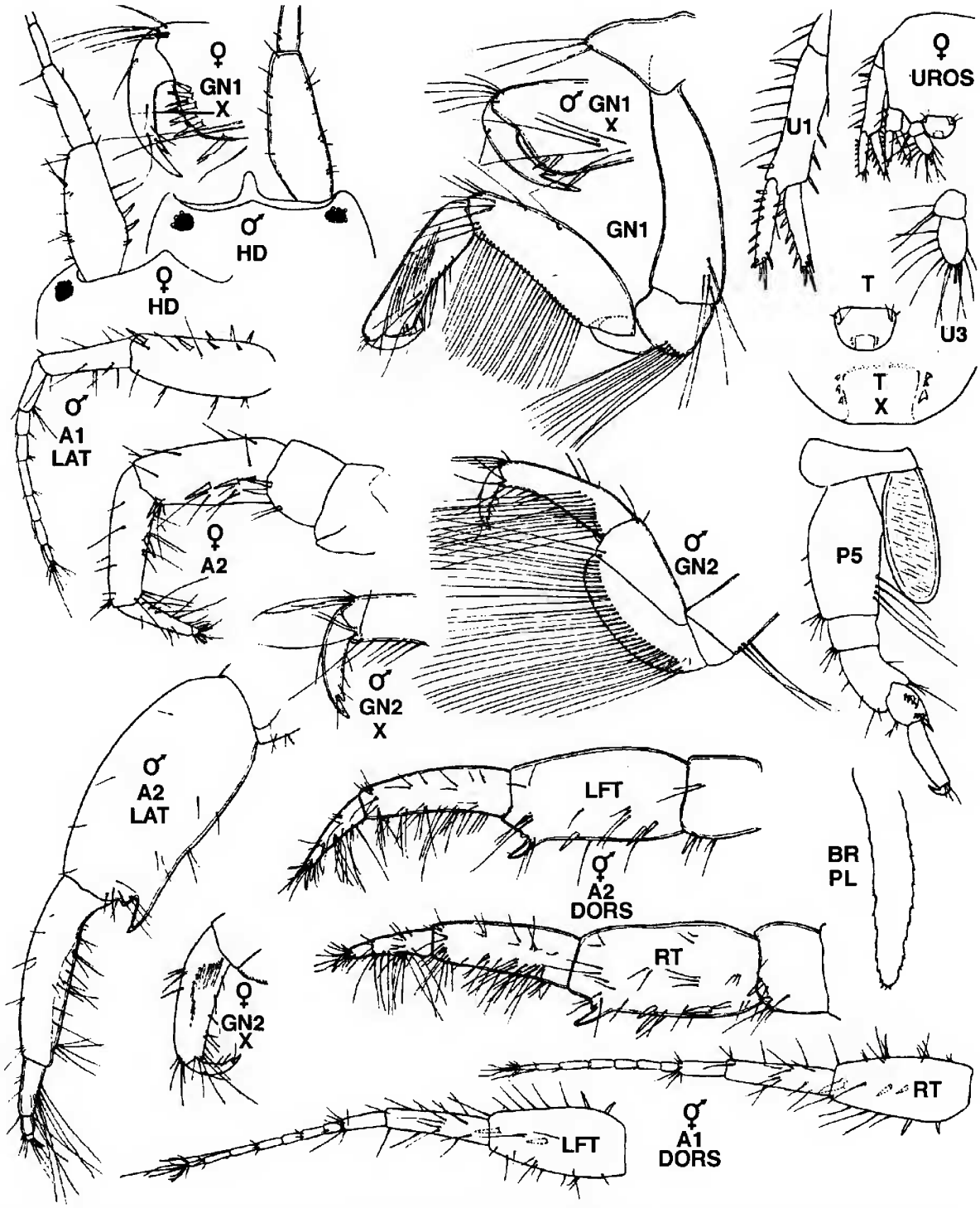

FIG. 22. ***C rassicorophium clarencense*** **(Shoem.). North Greenland. Male (4.0 mm); female (4.0 mm) (after Just, 1970).**

margin with 2 pairs of spines and several setae; flagellum medium, 3-segmented, moderately setose.

Gnathopod 1, propod slightly broadening distally; dactyl with small posterior marginal tooth, tip closing slightly beyond oblique palm. Gnathopod 2, basis stout; carpus short, posterodistal free margin lacking; propod long, with posterodistal cusp; dactyl slender, with small posterior marginal tooth.

Peraeopods 3 & 4 strong; basis broad, anterior margin weakly setose; segment 4 medium broad, partly overhanging short segment 5, anterior margin (of 4) nearly bare; dactyl slender, longer than segment 6. Peraeopod 5, hind margin of basis nearly bare. Peraeopod 7 moderately long; basis medium broad; margins of distal segments with short setae; dactyl short.

Pleon plates 1-3 weakly setose below. Uropod 1, outer

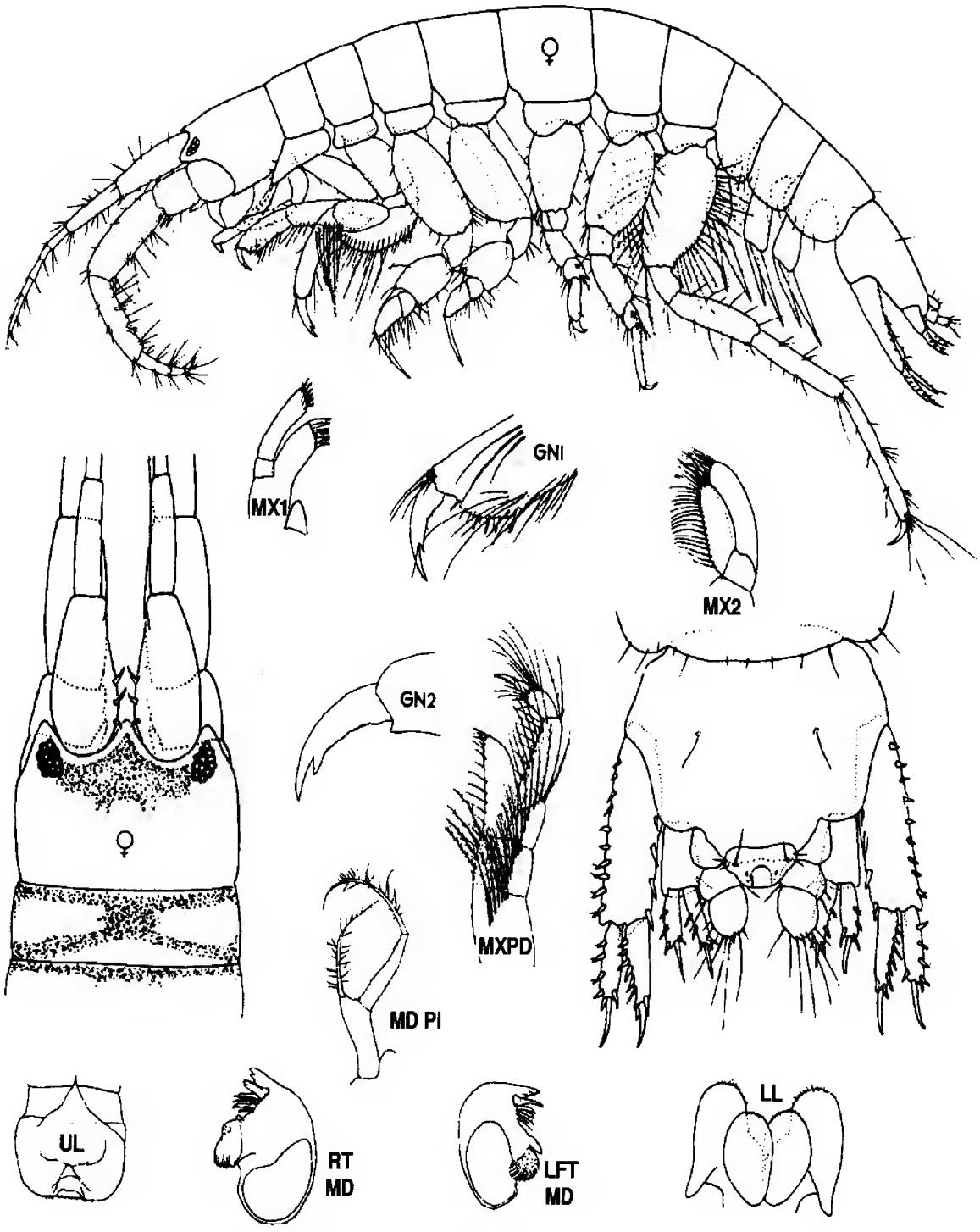

FIG. 23. *Crassicorophium bonelli* (M. E.). Outer coast, Nova Scotia. Female (4.5 mm) (after Bousfield, 1973).

margin of peduncle with short spines throughout; rami medium, subequal, each with 3-6 outer marginal spines. Uropod 2 medium; peduncular margins lacking spines; rami medium, each with 2 outer marginal pines. Uropod 3, peduncle broad, with small setose lateral lobe; ramus suborbicular, distal margin with long setae. Telson short, broad, with 4 posterodorsal pairs of small hook spines.

Brood lamellae slender, with gaps between each (Shillaker & Moore, 1987).

Adult male (3.8 mm): A presumed juvenile male (2.3 mm) from Ireland was described and illustrated by Myers et al (1989). The dactyls of gnathopods 1 & 2 conform closely

KEY TO SPECIES OF *HIRAYAMAIA*, NEW GENUS

1. Gnathopod 2, dactyl posteriorly bidentate; uropod 2, peduncular margins spinose ..... *H. tridentia* (Hirayama) (Fig. 25)
—Gnathopod 2, dactyl with 1 posterior marginal tooth; uropod 2, peduncular margins bare ..... 2.

2. Urosome, lateral margins convex; uropod 3, ramus suborbiculate ..... *H. hongkongensis* (Hirayama)
—Urosome, lateral margins straight; uropod 3 subovate, longer than wide ..*H. mortoni* (Hirayama)(Fig. 24)

with those of the adult female. In antenna 2, peduncular segment 4 bears a single-toothed distal process, and segment 5 has a small proximal medial marginal process.

Taxonomic and distributional commentary. The species is widely boreal and subarctic in the North Atlantic and northwestern North Pacific Tatar Strait, northern Sea of Japan)(Kudrjaschov, 1979; Ishimaru, 1994); recorded recently from the Bering Sea coast of Alaska by O'Clair (Coyle & Mueller (1981).

The species has not previously been recorded from the present study region (e.g., in Otte, 1976; Austin, 1985) nor found in study materials here.

Distributional ecology. Gurjanova (1951) interpreted previous distributional records of *C. bonelli* as those of a cosmopolitan species, widespread in temperate and tropical waters of both hemispheres. However, records from warm-water localities are probably attributable to females of superficially similar species, especially *Monocorphium insidiosum,* as Crawford (loc. cit.) so ably demonstrated. Authentic records of *C. bonelli* are restricted to arctic-boreal and boreal subregions of the northern hemisphere. Maximum abundance is reached in the Tatar strait region, in sandy shoals which border on the lower horizon of the littoral zone, and in deep cracks in rocks which have been blocked up with sand and overgrown with *Zostera marina* (Kudryaschov, loc. cit.).

The species is mainly hermaphroditic, males being extremely rare (Myers, et al., 1989). The life cycle is semi-annual, with two generations per year (Powell & Moore, 1991).

Hirayamaia new genus
(see Figs. 24, 25)

Corophium Latreille,1806, Hirayama, 1986: 449 (part).—Barnard & Karaman, 1991: 184 (part).

Type species. *Corophium mortoni* Hirayama, 1986 (present designation).

Species. *Hirayamaia hongkongensis* (Hirayama, 1986); *H. tridentia* (Hirayama, 1986).

Diagnosis. Urosome segments fused; lateral margins straight or convex, lacking distinct notch for uropod 1 that is inserted mainly ventrally. Head, rostrum short, weakly sexually dimorphic; inferior antennal sinus strongly regressed. Antenna 1 ordinary; peduncular segment 3 short. Antenna 2 strongly sexually dimorphic; gland cone small; segment 4 (male) large, pediform, posterodistal process bidentate; segment 5 , median and distal processes weak or lacking; flagellum short, with paired terminal spines.

Upper lip, epistome produced. Lower lip, mandibular lobes medium. Mandibular palp, basal segment with distal shelf or short process (type P4 or P5 of Hirayama, 1987b); spine row with 2-3 stout blades. Maxilla 1, palp slender. Maxilliped, outer plate slender, subcolumnar; palp segment 2 medium.

Gnathopod 1, carpus narrowing distally; propod, palm oblique, exceeded by weakly bidentate dactyl. Gnathopod 2, carpus medium, with small free lower margin beyond apex of fused shallow merus; propod, palm minute, with small cusp; dactyl short, with 1-3 posterior marginal teeth.

Peraeopods 3 & 4 short; basis variously broadened, glandular; segment 4 distally overhanging short segment 5. Peraeopods 5 & 6 short, bases unequal, that of peraeopod 5 lacking posterior marginal setae; segment 5 medium short; distal cluster with longish hook spines; segment 5 and dactyl variously reversed. Peraeopod 7 medium; basis little broadened; dactyl short.

Pleon plate 3, hind corner obtuse. Pleopod peduncles broader than deep; rami short, 6-7 segmented. Uropod 1, peduncle linear, outer margin spinose; rami straight, apices acute, one apical spine elongate, outer ramus the shorter. Uropod 2 short, rami slightly curved, lateral margins bare (or nearly so), acute apices with single long spine. Uropod 3, rami short, not strongly broadened, distal margin weakly setose. Telson short, broad, rounded.

Coxal gills narrow, sac-like, on peraeopods 3-6. Brood lamellae not described.

Etymology. The genus is named in honour of Dr. Akira Hirayama, in recognition of his outstanding contributions to the systematics of corophiin amphipods.

Distribution. Component species are endemic to shallow waters of the Hong Kong region of the South China Sea.

Taxonomic commentary. Species of the genus *Hirayamaia* cluster between those of the more primitive genus *Crassicorophium,* and the more advanced genus *Monocorophium* (Fig. 40, p. 133). Although many of *Hirayamaia* character states (e. g., form of the mandibular palp, propod and dactyl of gnathopod 2, and uropod 3) appear to be

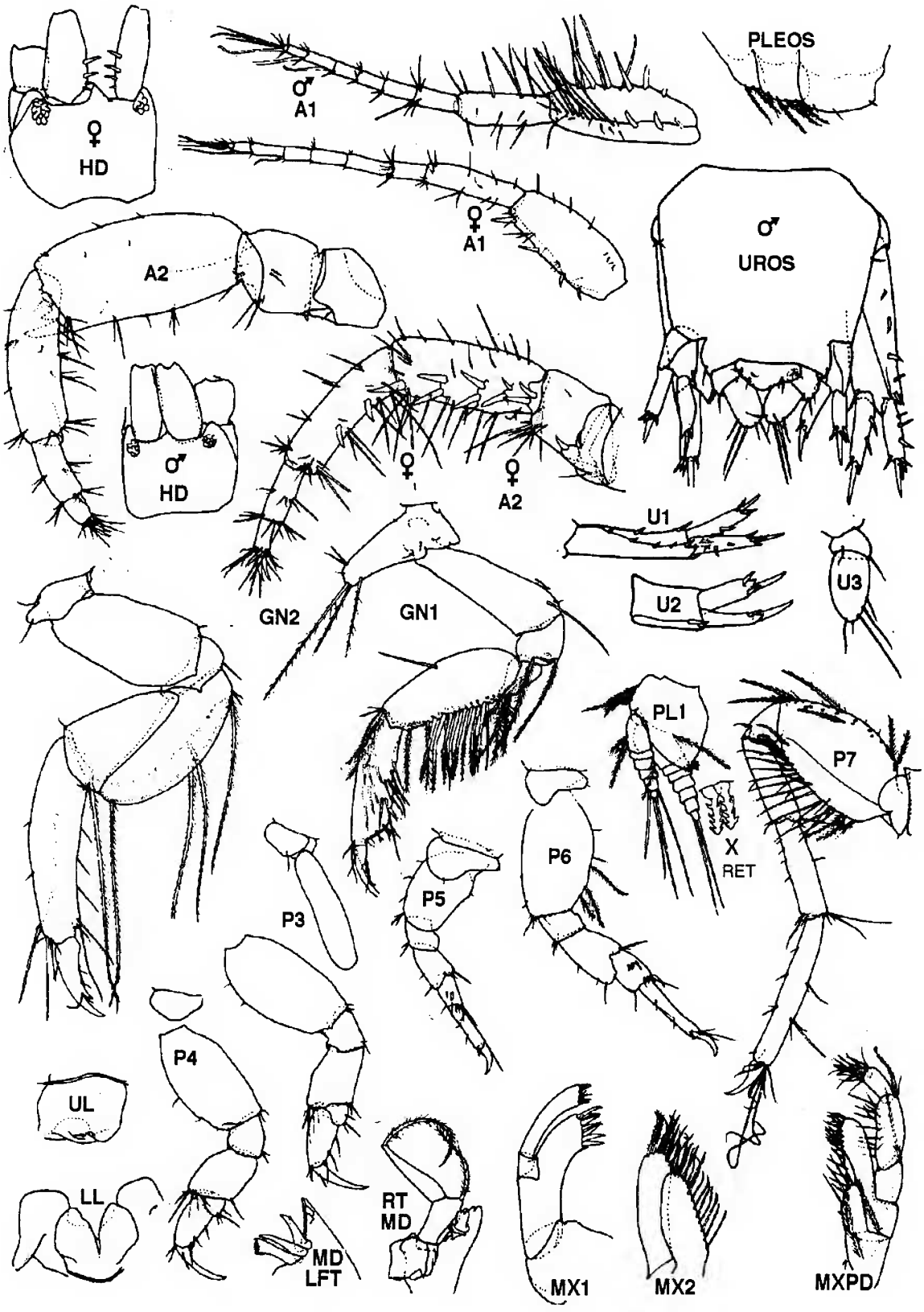

FIG. 24. ***Hirayamaa mortoni*** **(Hirayama). Hong Kong. Male (2.3 mm); female (3.0 mm) (after Harayama, 1986).**

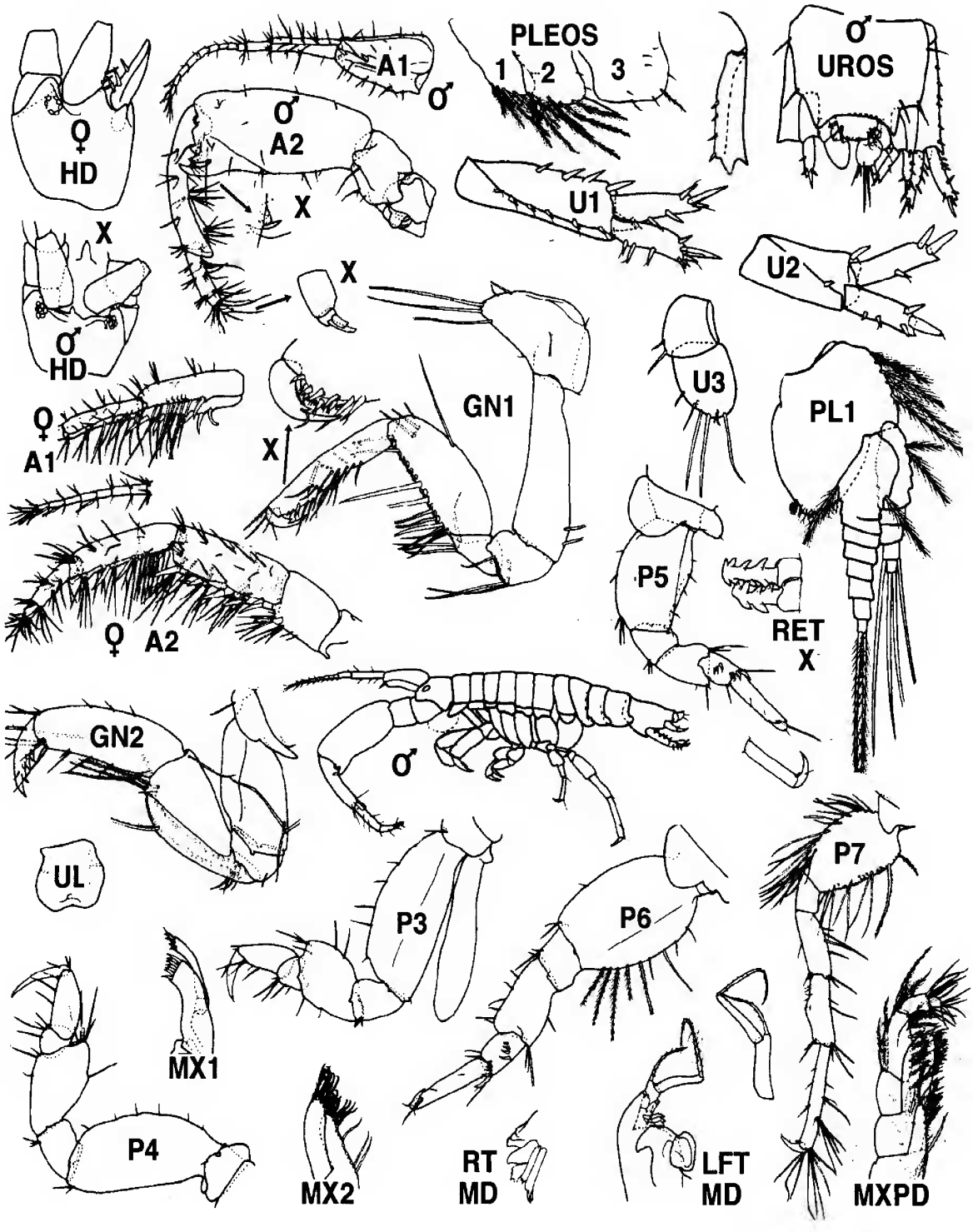

FIG. 25. ***Hirayamaia tridentia*** **(Hirayama). Hong Kong. Male (3.0 mm); female (4.8 mm) (after Hirayama, 1986).**

intermediate between the other two genera, its uniform (unnotched) lateral margin of the fused urosome segments is here considered an autapomorphy which, in combination with the advanced form of the mandibular palp, precludes direct ancestry with any other generic group treated herein.

***Monocorophium*, new genus**

Corophium Latreille, 1806, Stebbing 1906: 685 (part).—Crawford, 1937: 606 (Section B).—Chevreux & Fage, 1925: 363 (part).—Shoemaker, 1947: 47 (Section B.1, most).—Gurjanova, 1951: 684 (part).—Bousfield, 1973: 198 (part).—Lincoln, 1979: 522 (part).—Myers, 1982:185 (part).—Barnard & Karaman, 1991: 184 (part).—Ishimaru, 1994: 35 (part).

Type species. *Corophium insidiosum* Crawford, 1937 (present designation).

Species. *M. carlottensis*, n. sp. (p. 114); *M. steinegeri* (Gurjanova, 1951); *M. acherusicum* (Costa, 1857); *M. uenoi* (Steph-ensen, 1932); *M. tuberculatum* (Shoemaker, 1934b); *M. sextonae* (Crawford, 1937); *M. californianum* (Shoemaker, 1934a); *M. oaklandense* (Shoemaker, 1949).

Diagnosis: Urosome segments fused; uropods arising from lateral notches. Head, rostrum distinct; anterior margin sexually dimorphic. Antenna 1, segment 3 short. Antenna 2 strongly pediform, variously (or not) sexually dimorphic; segment 4 (male), with bidentate distal process; segment 5 usually with proximomedial tooth; distal process weak or lacking; gland cone short, relatively inconspicuous; flagellum short, 3-segmented, with apical paired spines.

Upper lip, epistome little (or not) produced. Lower lip, mandibular lobes strong. Mandible: spine row moderate (3-5 blades; palp of intermediate form [type P4 of Hirayama (1987b)]. Maxilliped, inner plate short to medium, apex subacute; outer plate slender, medial margin setose throughout; palp segment 2 medium to short.

Gnathopod 1 medium subchelate; dactyl denticulate behind, or tip weakly bidentate, exceeding short oblique palm. Gnathopod 2, merus not covering small anterodistal portion of carpus; dactyl short, tri- or quadridentate.

Peraeopods 3 & 4 short, bases broad (glandular); segment 4 expanded, often setose anteriorly; segment 5 short, overhung by segment 4. Peraeopods 5 & 6 short, segments 4 and 5 short, the latter with 2 clusters of short strong hook spines; segment 6 and dactyl reversed. Peraeopod 7 not elongate, basis medium broad; dactyl medium.

Pleon plate 3, hind corner rounded. Pleopod peduncles stout, wider than deep. Uropods 1 and 2, peduncle stout, widening distally; rami short, spinose laterally and apically, apices curved, acute. Uropod 3, ramus short, broad.

Telson short, wide, with dorsal hooks. Coxal gills slender, sac-like, on peraeopods 3-6. Brood lamellae relatively large, broad, margins with few setae.

Etymology. Combining the Greek prefix *mono* - one, and the generic root *Corophium*, with reference to the fused, one-segmented urosome.

Distributional ecology: Mostly tube-building species, of temperate-tropical affinities, but a few (*M. carlottensis, M. steinegeri*) are boreal and subarctic.

Taxonomic commentary. This relatively large subgroup was first recognized by Crawford (1937). At that time the complex comprised *C. insidiosum, C. tuberculatum, C. bonelli, C. sextonae, C. uenoi, C. acherusicum , C. crassicorne* and *C. californianum.* The group may be polyphyletic, the main subgroup arising from a *triaeonyx*-like ancestor with unfused urosome segments.

Within the genus *Monocorophium* , the *insidiosum* subgroup (above) is characterized by a strongly sexually dimorphic rostrum, type P4 mandibular palp, tri- or quadridentate dactyl of gnathopod 2, and short, broad ramus of uropod 3.

A second subgroup, of *C. californianum* and *C. oaklandense*, encompasses a pair of closely related species endemic to the Pacific coast of North America, in which antenna 2 is strongly pedamorphic in both sexes (p. 123). *C. miospinulosum,* a minute burrowing species assigned to Crawford's section B by Hirayama (1986), is here recognized as generically distinct at a more primitive level (Fig. 41, p.133).

Corophium ellisi Shoemaker, 1934b, has fused urosomal segments but otherwise conforms closely with the diagnosis of the genus *Americorophium* (see p. 90). The Indo-Pacific species *C. triaeonyx*, with urosome segments free, conforms partially with the genus *Americorophium* on the one hand, and *Monocorophium* on the other. It may prove to be a living "missing link" that transcends the otherwise sharp taxonomic distinction between genera with urosome segments separate and those with segments fused.

Monocorophium insidiosum (Crawford)
(Figs. 26, 27)

Corophium insidiosum Crawford, 1937: 615, fig. 2a-g.—Shoemaker, 1947: 53, figs. 6, 7.—Barnard, 1970: 101, fig. 54.—Bousfield, 1973: 203, fig. LXII.1.—Barnard, 1975: 338-340 (key), figs. 142, 145.—Otte, 1976: 6 (key), figs. 6, 7.—Carlton, 1979: 658.—Lincoln, 1979: 530, figs. 254d-h.—Hirayama, 1984: 14.—Austin, 1985: 615.—Barnard & Karaman, 1991:185.—Ishimaru, 1994: 35.
Corophium cylindricum Say, 1818: 287(?).

Material Examined. About 85 specimens in 25 lots:
BRITISH COLUMBIA.
Vancouver Island and southeastern mainland coast. ELB Stns, 1955: G13(10), M1(3), P7(5). ELB Stns, 1959: O6(Louis Creek lagoon) - 14 spms incl. male (5.2 mm) (**fig'd**); female (4.8 mm) (**fig'd**), CMN Cat. No. NMCC1992-0848. N23(2), V27(1), N18(1). ELB Stns, 1970: P701(1), P702(1), P706(7), P719(4), P721(4). ELB Stn, 1975: P26(2).
J.F.L. Hart Stn, Victoria, 1928 -1 specimen.
K. Conlan Stns, Saanich Inlet, 1975: 1104S- 4 specimens.

WASHINGTON.
Inner coast. ELB Stn, Friday Harbor, 1955: M13(1).
Outer coast. ELB Stns, 1966: W22(3); W29(13).

KEY TO SPECIES OF *MONOCOROPHIUM*

1. Antenna 2 strong, segment 4 with distal bidentate process in both male and female; peraeopod 3, basis narrower than in peraeopod 4 ..... 2.
—Antenna 2 strong in male but smaller, lacking bidentate distal process in female; peraeopods 3 & 4, bases subequally broad ..... 3.

2. Antenna 2, distal process of peduncular segment 5 very strong, length ~flagellar segment 1; peraeopod 7, basis narrow, width ~1/2 length; uropod 1, peduncle with few (3-5) outer marginal spines. ..... *M. californianum* (Shoem.) (p. 123)
—Antenna 2, distal process of peduncular segment 5 short, >1/2 flagellar segment 1; peraeopod 7, basis broad, width ~ length; uropod 1, peduncle with 8-10 outer marginal spines ..... *M. oaklandense* (Shoem.) (p. 123)

3. Rostrum (male) weak, not projecting beyond lateral head lobes; gnathopod 2, dactyl with 2 posterior marginal teeth; uropod 2, inner ramus, outer margin spines ..... 4.
—Rostrum (male) strong, projecting beyond lateral head lobes; gnathopod 2, dactyl with 3-4 posterior marginal teeth; uropod 2, inner ramus, outer margin bare ..... 6.

4. Gnathopod 1, dactyl short, thick, barely overlapping palm; uropod 1 spinose, rami with 6-8 outer marginal spines ..... *M. sextonae* (Crawf.) (p. 120)
—Gnathopod 1, dactyl slender, distinctly exceeding palm; uropod 1, rami with 4 outer marginal spines . 5.

5. Antenna 2 (both sexes), posterior margin of peduncle and flagellum strongly setose; peraeopods 3 & 4, anterior margin of segment 4 setose; North Atlantic ..... *M. tuberculatum* (Shoem.)
—Antenna 2, posterior margin of segments weakly setose; peraeopods 3 & 4, segment 4 anterior margin nearly bare; North Atlantic, synanthropic in North Pacific ..... *M. acherusicum* (Costa) (p. 117)

6. Rostrum (male) short, projecting slightly beyond lateral head lobes; urosome, lateral notch small, uropod 1 inserted mainly ventrally; gnathopod 1, dactyl greatly (50%) exceeding palm . *M. uenoi* (Steph.) (p. 119)
—Rostrum (male) long, tip projecting distinctly beyond lateral head lobes; urosome with distinct lateral notches, uropod 1 inserted mainly laterally; gnathopod 1, dactyl short, tip little exceeding palm. ..... 7.

7. Peraeopods 3 & 4, anterior margins of basis and segment 4 weakly (or not) setose; peraeopod 7 elongate, segment 6 with elongate distal setae ..... *M. carlottensis*, n. sp. (p. 114)
—Peraeopods 3 & 4 (esp. in male), anterior margins of basis and segment 4 strongly setose; peraeopod 7 relatively short, segment 6 with short distal setae ..... 8.

8. Pleosome segment 3 with short posterodorsal tufted process; uropod 2, outer ramus with distinct outer marginal spine ..... *M. insidiosum* (Crawf.) (p. 111)
—Pleosome segment 3 lacking distinct tufted mid-dorsal process; uropod 2, outer ramus lacking outer marginal spine ..... *M. steinegeri* (Gurj.) (p. 116)

Diagnosis. Male (4.0 mm). Pleosome segment 3 with low posterior median tufted process or hump. Urosome with distinct lateral notch; uropod 1 inserted mainly laterally. Head, rostrum elongate, tip distinctly exceeding lateral head lobes. Antenna 1, peduncular segment 1 with inner marginal conical process; flagellum 7-8 segmented. Antenna 2 strongly pediform; peduncular segment 5 not shorter than 4, with small proximal median tooth and distal process; flagellum 3-segmented, posterior margin strongly setose.

Gnathopod 1, dactyl tip little exceeding palm. Gnathopod 2, basis stout; carpus short, with short postero-distal free margin; propod lacking postero-distal cusp; dactyl with 3 unequal posterior marginal teeth.

Peraeopods 3 & 4, anterior margin of basis and segment 4 moderately to strongly setose; dactyls curved, shorter than segment 6. Peraeopods 5 & 6, bases setose postero-distally. Peraeopod 7 not elongate, basis medium broad; distal segments weakly setose; dactyl short.

Uropod 1, rami short, unequal, each with 3 outer marginal spines. Uropod 2 short, outer ramus with 1 outer margin spine, inner ramus bare. Uropod 3, peduncle with small setose lateral lobe. Telson broader than long, with 4 postero-dorsal pairs of small hook spines.

Female (3.8 mm). Rostrum short, not exceeding lateral head lobes. Antenna 1, peduncular segment 1 with 3-4 proximomedian spines. Antenna 2, peduncular segments short, stout; segment 4, posterior margin with 3 pairs of strong spines; flagellum weakly setose posteriorly.

Peraeopods 3 & 4, anterior margins of basis and segment 4 relatively sparsely setose.

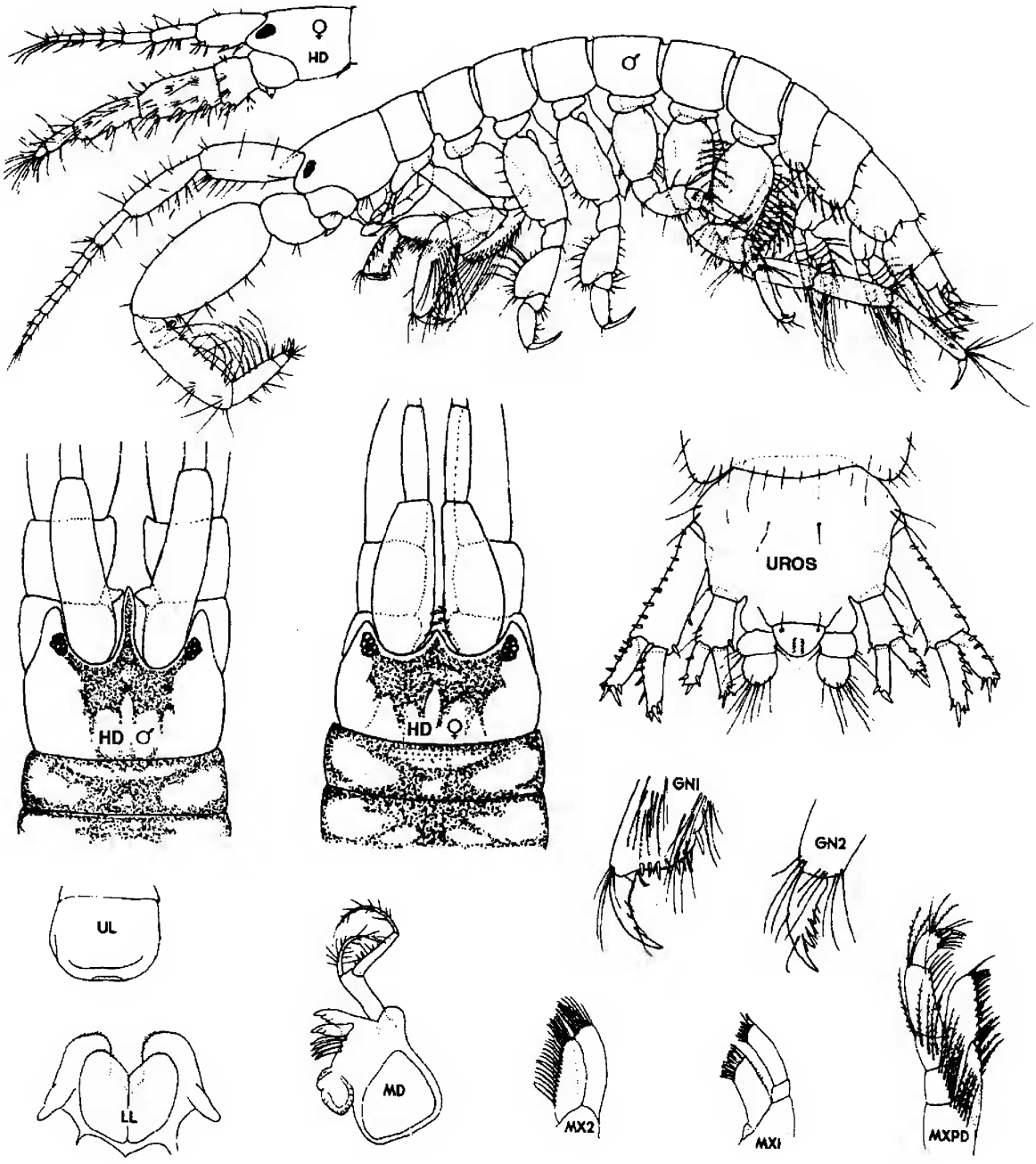

FIG. 26. ***Monocorophium insidiosum*** **(Crawford). Southwestern Gulf of St. Lawrence Male (4.0 mm); female (4.5 mm) (after Bousfield, 1973).**

Brood lamellae relatively short and slender, with few (<20) marginal setae.

Taxonomic and distributional commentary. Specimens of *Monocorophium insidiosum* from the North American Pacific region differ slightly from those of the North American Atlantic region in their slightly larger size at maturity, and generally more strongly setose appendages.

The species is considered native to the North Atlantic region from whence it has presumably been transported by commercial vessels to the North Pacific. The species has been widely recorded from the Strait of Georgia and Puget Sound, south to central California (Carlton, 1979).

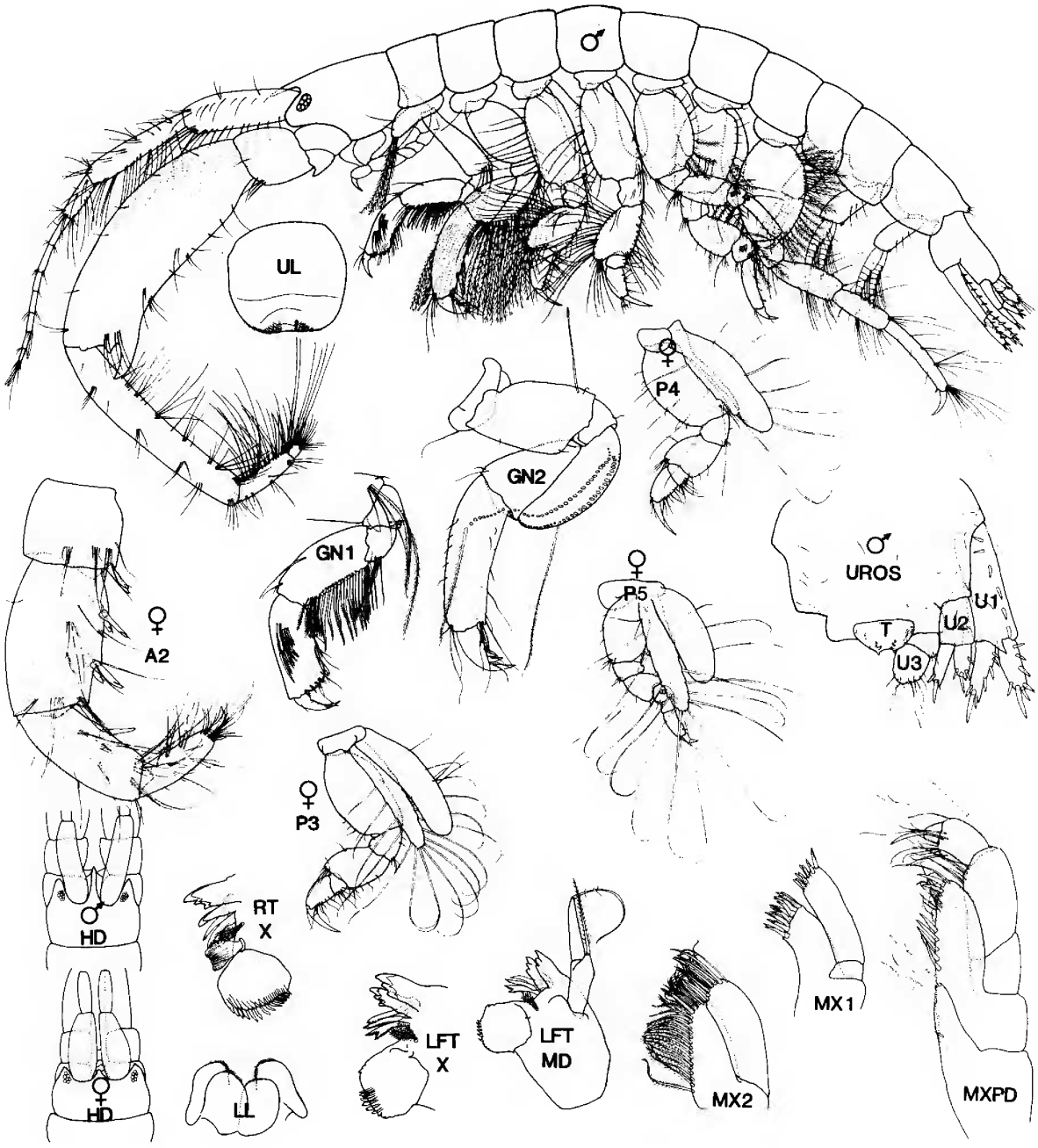

FIG. 27. *Monocorophium insidiosum* (Crawford). Louis Creek lagoon, B. C.. Male (5.2 mm); female (4.8 mm).

Taxonomic and distributional commentary. *Monocorophium insidiosum* is endemic to temperate to warm-temperate waters of the North Atlantic region (Bousfield, 1973). On the basis of distributional overlap, *M. insidiosum* may prove synonymous with *C. cylindricum* Say, 1818, for which the type material is apparently not extant. Carlton (loc. cit.) has summarized synanthropic records of *M. insidiosum* from the Pacific coast of North America, including central and northern California, Washington, and British Columbia. The latter records are encompassed by Otte (1976) and Austin (1985). The species is apparently synanthropic in Hawaii (Barnard, 1970) and Japan (Hirayama, 1984; Ishimaru, 1994).

Monocorophium carlottensis, new species
(Fig. 28)

Corophium insidiosum (Crawford) f. Staude, 1987: 351 (key), 386.—Barnard, 1975: 338-340 (key)?.—Otte, 1976: 6 (part).—Austin, 1985: 615.

Material Examined: About 290 specimens in 29 lots, mostly from tide pools and brackish waters, from Prince William Sound and S.E. Alaska, through the Queen Charlotte Islands, and north-entral coast, scarcer to S. Vancouver I., but none southwards in Washington State.

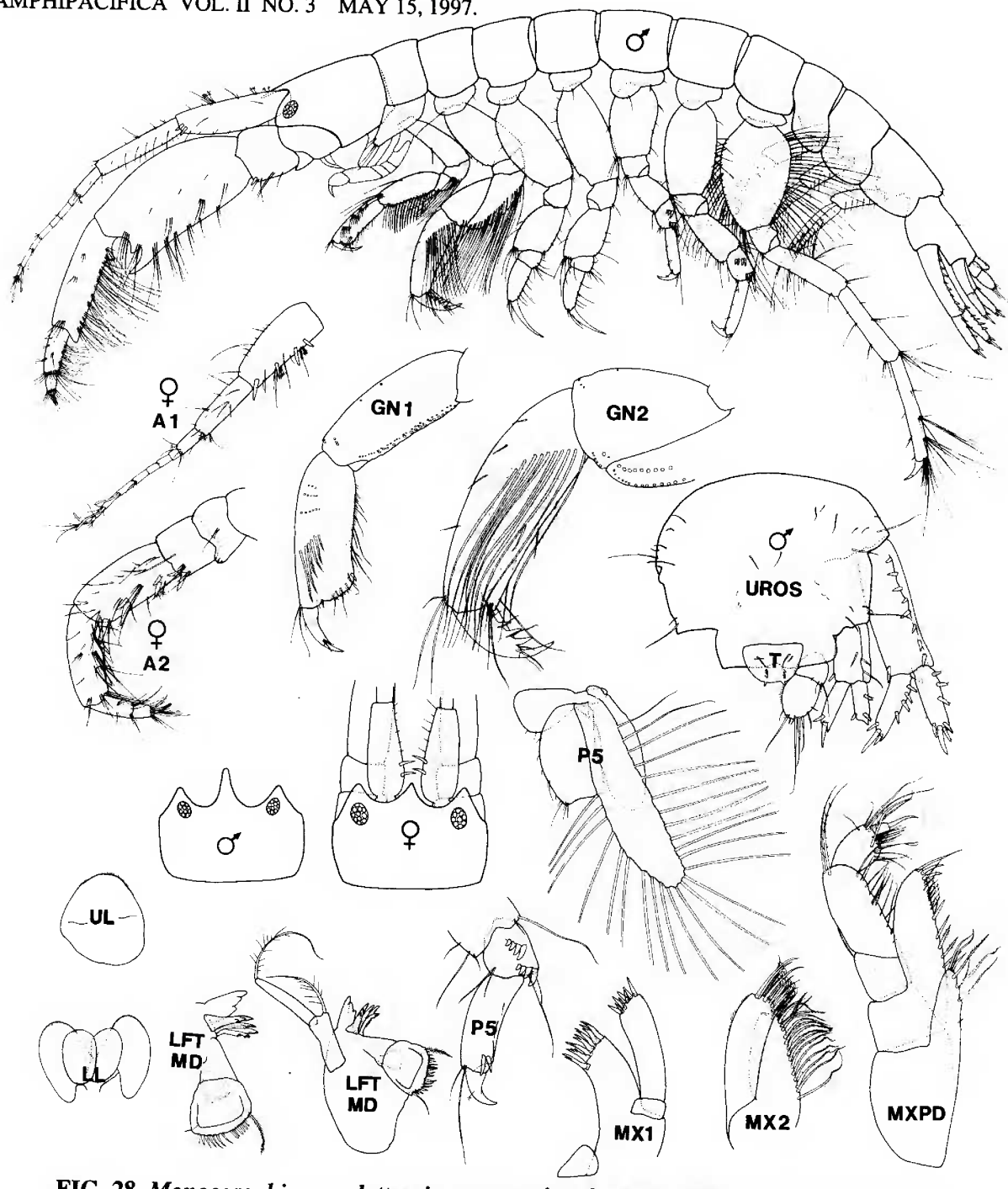

FIG. 28. ***Monocorophium carlottensis*****, new species. Codfish Pass, B. C. Fem. (4.2 mm). Island Bay, Q. C. I. Male (3.0 mm).**

ALASKA.

Southeastern Alaska. ELB Stns, 1961: A3(2), A70(1), A86(4), A91(1), A92(2), A96(7), A105(2), A131(1).

ELB Stn. S23F1 (Taigud I, Baranof I.), 1980 - 14 females, 4 im, CMN Cat. No. NMCC1992-0985.

BRITISH COLUMBIA.

Queen Charlotte Islands. ELB Stns., 1957: H2, H2b(4), H8b(8), E5(1), E14c(10), W3a(3). J Scoggan Stn 68-155, Island Bay, 1968 - male (3.0 mm), slide mount, **allotype**, 2 males, 6 females, CMN Cat No. NMCC1992-0943.

North-central mainland coast. ELB Stns., 1964: H5(7), H6(6), H12(1), H25(3), H26(7), H30(>50), H31(3), H36(10), H39(1), H47(Codfish Bay) - female ov. (4.2 mm), slide mount, **holotype**, 50 **paratypes**, CMN Cat. No. NMCC1992-0777, H48(1), H50(4), H53(11), H59(5).

Diagnosis. Male (3.0 mm): Pleosome segment 3 with small posterior median tufted process or hump. Urosome with distinct lateral notch; uropod 1 inserted mainly laterally. Head, rostrum elongate, tip distinctly exceeding lateral head lobes. Antenna 1, peduncular segment 1 with weak inner marginal conical process; flagellum short, 7-8 segmented. Antenna 2 stoutly pediform; peduncular segment

5 shorter than 4, with prominent distal process, posterior margin with small proximal median tooth and densely lined with longish setae; flagellum very short, 3-segmented, posterior margin moderately setose.

Gnathopod 1, dactyl tip little exceeding palm. Gnathopod 2, basis medium broad; carpus short, with distinct free posterodistal margin; propod with posterodistal cusp; dactyl with 3 unequal posterior marginal teeth.

Peraeopods 3 & 4, anterior basis and segment 4 moderately broadened setose, anterior margins weakly (or not) setose; dactyls slender, longer than segment 6. Peraeopod 5, basis virtually lacking posterior marginal setae. Peraeopod 7 somewhat elongate, basis medium broad; segment 6 with 3 posterodistal clusters of long setae; dactyl short.

Pleon plates 1-3 weakly (or not) setose below. Uropod 1, rami short, subequal, each with 3 outer marginal spines. Uropod 2 short, outer ramus with 1 outer marginal spine; inner ramus bare. Uropod 3, peduncle lacking lateral lobe. Telson short, broad, with 3-4 posterodorsal pairs of small hook spines.

Female (4.2 mm): Rostrum short, broad, tip about level with apex of lateral head lobes. Antenna 1, peduncular segment 1 with 2 proximo-medial spines. Antenna 2, peduncular segments short, stout; segment 4, posterior margin with 3 pairs of medium spines; segment 5 and flagellum moderately setose posteriorly.

Peraeopods 3 & 4, anterior margins of basis and segment 4 relatively sparsely setose.

Brood lamellae broadly strap-like, with moderate numbers (~25) of marginal setae.

Etymology. The species name recognizes its regional centre of distribution in the Queen Charlotte Islands, British Columbia.

Distributional ecology. From Prince William Sound and southeastern Alaska, south to the Queen Charlotte Islands and the north-central mainland coast of B. C. On kelp, eel grass and stones, over mud and sand, mainly along surf-protected shores, from LW level to depths of 10 m, in summer water temperatures of ~10-15‰ .

Taxonomic commentary. *Monocorophium carlottensis* is a member of the *insidiosum-uenoi* group characterized by an elongate rostrum and heavy distal antennal setation in the male. It differs markedly from the Pacific regional *M. uenoi* and from the Atlantic regional *M. insidiosum* in characters of the key to species (p. 112).

The species is also similar to *M. steinegeri* but differs in its distinctly smaller size and less heavy armature of antennae and peraeopods.

The overall morphological similarity of *M. carlottensis* and *M. insidiosum* might justify sibling species designation. However, *M. carlottensis* has markedly more tightly setose antenna 2, and weakly setose peraeopods 3 & 3 (male). It is also smaller in size, and distributionally non-overlapping.

Monocorophium steinegeri (Gurjanova)
(Figs. 29)

Corophium steinegeri Gurjanova, 1951: 979, fig. 682.—Kudrjaschov, 1979: 126.—Barnard & Karaman, 1991: 186.

Material Examined. About 225 specimens in 8 lots.
ALASKA.
Aleutian Islands. N.A. Powell Stn., Unimak I., Izembek Lagoon, 1969: ~200 specimens. (male, female, **fig'd**) NMCC-1992-0749.
Southeast Alaska. ELB Stns., 1961: A19(1), A139(1).

BRITISH COLUMBIA.
Queen Charlotte Islands. ELB Stns, 1957: H4 (9 males, 3 females, 3 imm).
North-central mainland coast. ELB Stn, 1964: H25(3)

Diagnosis. Male (6.0 mm). Pleosome segment 3 with trace posterior median tufted process. Urosome with distinct lateral notch; uropod 1 inserted partly ventrally.

Peraeopods 3 & 4, anterior margin of basis and segment 4 strongly setose; dactyl curved, shorter than segment 6. Peraeopod 5, bases weakly setose posterodistally. Peraeopod 7 not elongate; basis nearly as broad as deep.

Pleopod peduncles very broad, width nearly twice length. Uropod 1, rami short, subequal, each with 4-5 outer marginal spines. Uropod 2 short, rami lacking marginal spines. Uropod 3, peduncle with small setose lateral lobe. Telson slightly broader than long.

Female (to 5.5 mm): Rostrum short, broad, not exceeding lateral head lobes. Antenna 1, peduncular segment 1 with small spined median process. Antenna 2, peduncular segments short, stout; segment 4, posterior margin with 3 pairs of strong spines; segment 5 with single median posterior pair of spines; flagellum very short, weakly setose posteriorly.

Peraeopods 3 & 4, anterior margins of basis and segment 4 relatively less strongly setose than in male.

Brood lamellae long, strap-like, with moderate numbers (25-35) of marginal setae.

Taxonomic commentary. Specimens of *Monocorophium steinegeri* from the North American Bering Sea region differ very little from specimens from the coast of Kamchatka described and figured by Gurjanova (1951). The species appears most closely related to *M. insidiosum* and *M. carlottensis*.

Distributional ecology. Eastern Kamchatka, northern Sea of Okhotsk and the Bering Sea, from LW level littorally and sublittorally on sand. Characterized by Kudrjaschov (loc. cit.) as a high-boreal Asiatic Pacific species for which the northern part of the Tatar Strait is probably the extreme southern boundary of distribution.

On the North American Pacific coast, it occurs sporadically south to the Queen Charlotte Islands.

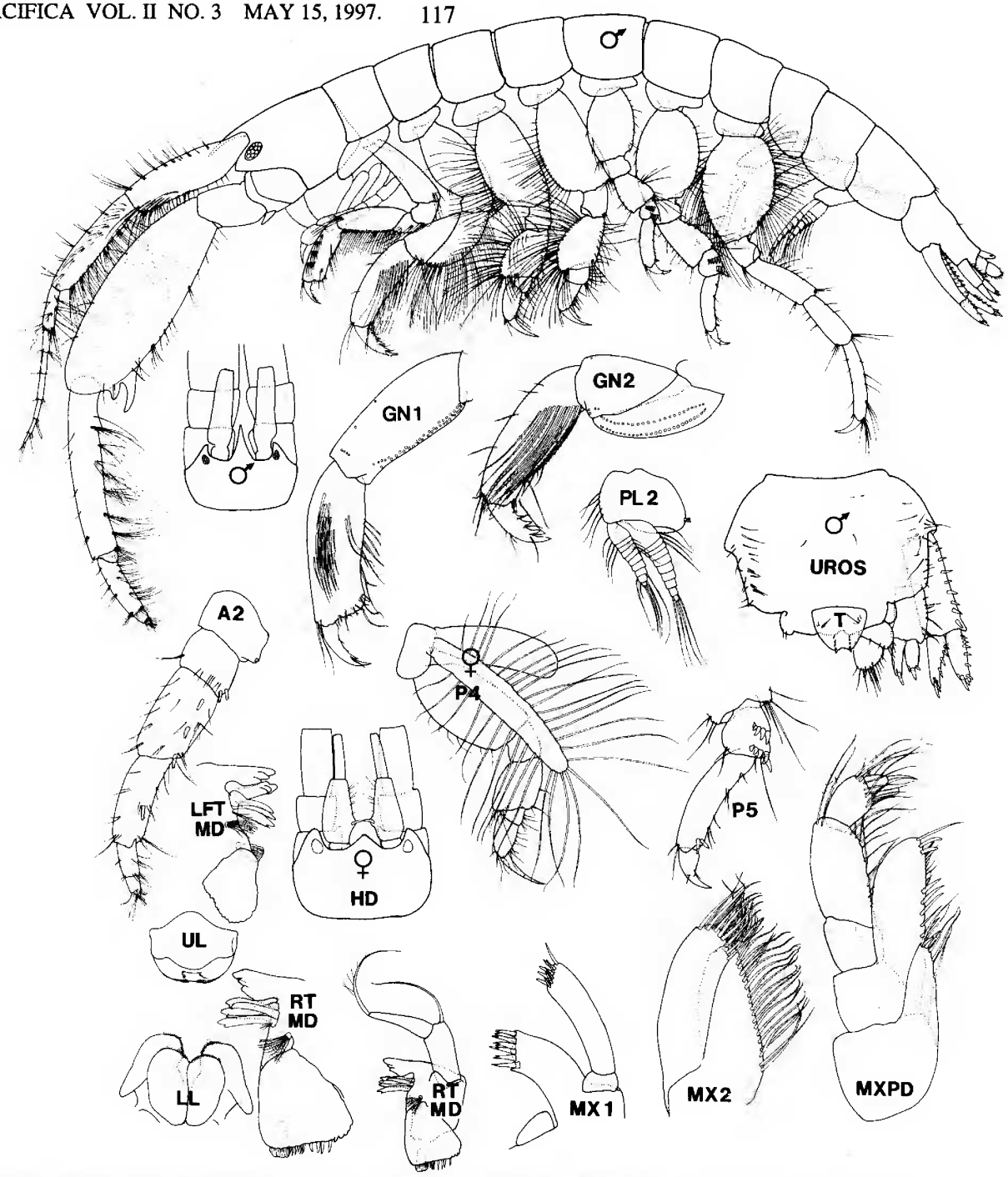

FIG. 29. ***Monocorophium steinegeri*** **(Gurjanova). Aleutian Is . Male (6.0 mm); female (6.0 mm).**

Monocorophium acherusicum (Costa)
(Figs. 30)

Corophium acherusicum Costa, 1851: 232.—Shoemaker, 1947: 53, figs. 2, 3.—Shoemaker, 1949: 76.—Bousfield, 1973: 201, Pl.LXII.2.—Barnard, 1975: 338-340 (key), figs. 143, 144, 147.—Otte, 1976: 8 (key), figs. 6, 7.—Carlton, 1979: 655 (distribution list, Alaska to California).– Hong, 1983: 135, figs. 6-8.—Hirayama, 1984: 13.—Austin, 1985: 615.—Staude, 1987: 386, fig. 18.27.—Kim, 1991: 114, fig. 26—Ishimaru, 1994: 35.

Corophium acherusicum Costa (nomen nudum) Stebbing, 1906: 692.—Barnard & Karaman, 1991: 185.

Material Examined.

BRITISH COLUMBIA.

Southern Vancouver Island and southeastern mainland.. ELB Stns., 1955: P9(3), G20(1), M1(5). ELB Stns.,1970: P709(15), P712(6). ELB Stns, 1972: P2(>50), P6(4), P6a(2), P6c(1), P18a(11). ELB Stmns., 1977: B6b(3), B7(1). JFL Carl Stn, 1938. Berkley Beach, Departure Bay - 1 spm; Ibid, 1931. Stn 2242 - 5 specimens; K. Conlan, Stns, 1977. French Creek, Stn. FC-1(2); Stn. FC-11(1); coll. unknown, 1987. Stn 87 Sepping I, Barkley Sd.- 2 specimens; D.V. Ellis Stns., 1976.: Stn. 4 (Tsable Estuary) - 4 specimens; Stn 7 (Chemainus Estuary) - 1 specimen.

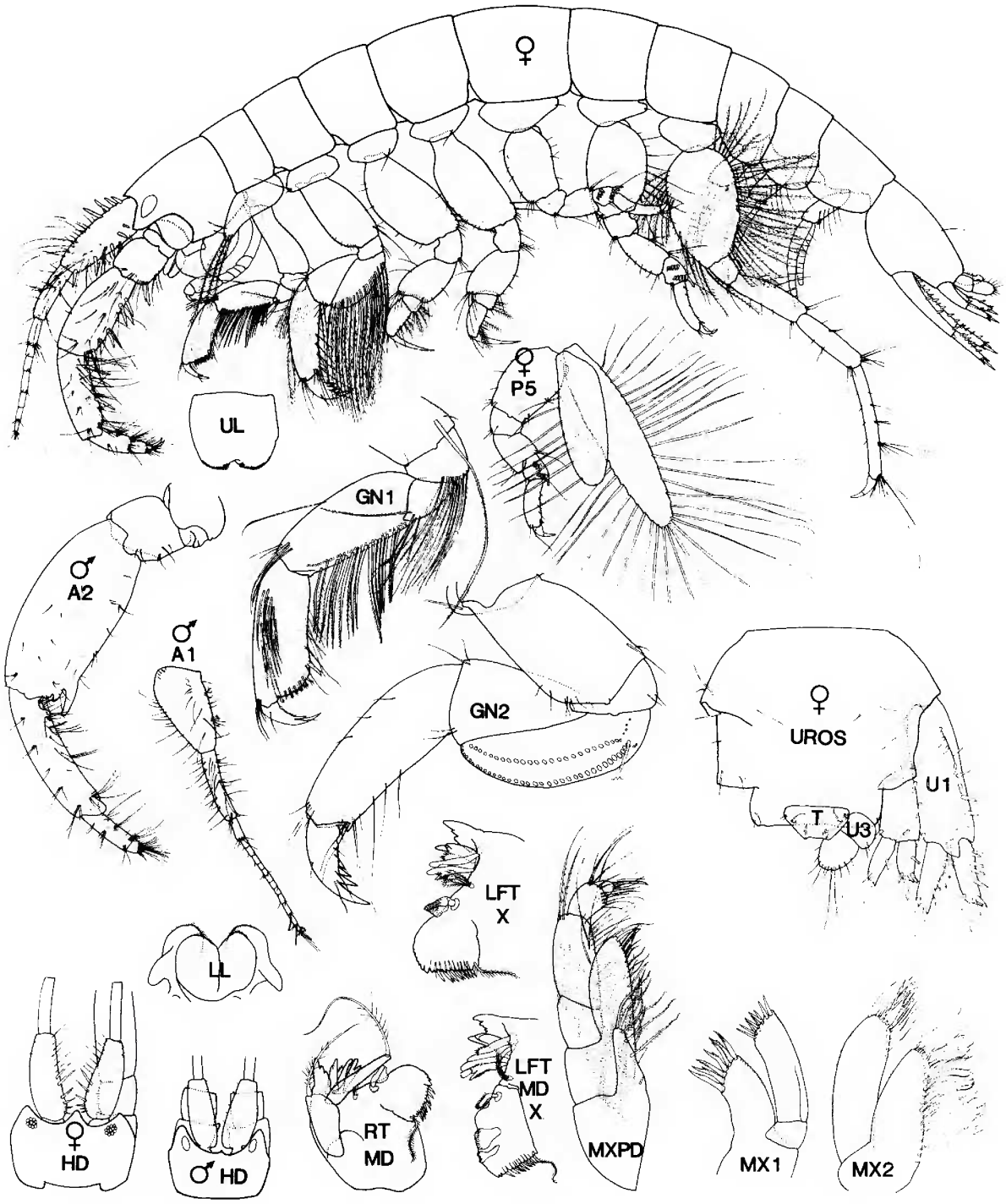

Fig. 30. ***Monocorophium acherusicum*** **(Costa). Steamboat I., WA. Male (4.0 mm); female (4.2 mm).**

WASHINGTON-OREGON:

Washington. ELB Stns, 1966: W3(15); W4(2); W8 (442); W10(42); W12(51); W13 (Steamboat I.) - 55 spmns incl. male (4.0 mm) (**fig'd**); female ov. (4.2 mm) (**fig'd**), CMN Cat. Nos. NMCC1992-0744+0785; W30(22); W35(many); W44(32).

Oregon. ELB Stn 1966: W64 (63).

Diagnosis. Male (4.0 mm): Pleosome segment 3 dorsally smooth. Urosome with distinct lateral notch; uropod 1 inserted mainly laterally. Head, rostrum very short, recessed posterior to lateral head lobes. Antenna 1, peduncular segment 1 smooth, bulging proximally, narrowing distally; flagellum slender, 7-9-segmented. Antenna 2 strongly pediform; peduncular segment 5 shorter than 4, with broad distal process, posterior margin with small proximal tooth but few setae; flagellum, short, weakly setose.

Gnathopod 1, propod not narrowing distally; dactyl tip little exceeding palm. Gnathopod 2, basis medium broad; carpus short, deep, with distinct postero-distal free margin; propod with distinct postero-distal cusp; dactyl with 2-3 unequal posterior marginal teeth.

Peraeopods 3 & 4, basis broad, anterior margin bare; segment 4 medium, lacking anterior marginal setae; dactyl slender, longer than segment 6. Peraeopods 5, basis small, hind margin not setose. Peraeopod 7 not elongate, basis medium broad; segment 6 not strongly setose distally; dactyl short.

Pleon plates 1-3 weakly (or not) setose below. Uropod 1, rami short, unequal, each with 4-6 outer marginal spines. Uropod 2 short, rami each with 1(2) outer marginal spine(s). Uropod 3, peduncle with small nearly bare lateral lobe. Telson short, broad, with 3-4 postero-dorsal pairs of small hook spines.

Female (3.5 mm): Rostrum short, broad, apex about level with lateral head lobes. Antenna 1, peduncular segment 1 with numerous strong median and posterior spines. Antenna 2, peduncular segments short, stout; segment 4, posterior margin with 3 -4 pairs of strong spines; segment 5, posterior margin with 2 spine groups and clusters of setae; flagellum short, with whorls of setae.

Brood lamellae large, broadly strap-like; margins with numerous (35-40) setae.

Taxonomic and distributional commentary. Specimens of *Monocorophium acherusicum* from the North American Pacific region are similar to those of the western North Pacific (figured by Hong, 1983). However, they differ from those of the North American Atlantic region in their more heavily spinose antennae, more elongate dactyl of gnathopod 1, and more strongly dentate dactyl of gnathopod 2. At present these differences are considered only varietally or regionally significant since *M. acherusicum* is considered native to the North Atlantic region and widely synanthropic elsewhere.

Monocorophium acherusicum is more closely similar to *M. sextonae* (Crawford) and other more primitive members of the genus. However, morphological similarity with members of the genus *Crassicorophium*, especially with *C. bonelli* is here considered homoplasious (Fig. 40, p. 133).

Carlton (loc. cit.) has summarized records from the Pacific coast of North America, from Alaska to California, and Ishimaru (loc. cit.) from Japanese coastal waters where it is very probably commercially synanthropic. *M. acherusicum* is perhaps the most widely distributed species of corophiin amphipod in temperate-tropical waters of the world. Its region of endemicity is now difficult to pin-point. However, the eastern North Atlantic, from which it was originally described, seems the most probable source region.

Stebbing (loc. cit.), and Barnard & Karaman (loc. cit.) consider this species to be a nomen nudum. However, under the ICZN 50-year usage rule, the name is here considered sufficiently authentic to justify its formal recognition as a legitimate species name.

Monocorophium uenoi (Stephensen)
(Fig. 31)

Corophium uenoi Stephensen, 1932: 494, figs. 3, 4.—Barnard, 1964:130 (map).—Barnard, 1952a: 28, pls. 8,9.—Barnard, 1975: 338-340 (key), fig. 139.—Carlton, 1979: 660.—Chapman, 1988: 366.—Kim, 1991: 118, fig. 28.—Barnard & Karaman, 1991: 186.—Ishimaru, 1994: 36.

Diagnosis. Male (to 5.0 mm): Pleosome segment 3 essentially smooth dorsally. Urosome with indistinct lateral notch and slightly marginal concavity; uropod 1 inserted mainly ventrally. Head, rostrum slightly exceeding lateral head lobes. Antenna 1, peduncular segment 1 with very low inner marginal swelling; flagellum slender, 8-9 segmented. Antenna 2 strongly pediform; peduncular segment 5 not shorter than 4, with prominent distal process, posterior margin with small proximal median tooth and 5-6 clusters of longish setae; flagellum short, 3-segmented, posterior margin strongly setose.

Gnathopod 1, dactyl slender, tip greatly (50%) exceeding short palm. Gnathopod 2, basis very stout; carpus short, deep, with distinct free posterodistal margin; propod lacking posterodistal cusp; dactyl with 3 unequal posterior marginal teeth, middle tooth often strongest.

Peraeopods 3 & 4 very short, basis broad, anterior margin nearly bare; segment 4 very broad, totally overhanging short segment 5, anterior margin moderately setose; dactyls curved, shorter than segment 6. Peraeopod 5, posterior margin of basis nearly bare. Peraeopod 7 not elongate; basis medium broad; segment 6 with longish posterodistal setae; dactyl curved, subequal in length to segment 6.

Pleopod peduncles very broad, rhomboidal, width nearly twice length. Uropod 1, rami short, unequal, each with 3-4 outer marginal spines. Uropod 2 short; rami unequal, outer ramus with 1-2 outer marginal spine, inner ramus often bare. Uropod 3, peduncle with small setose lateral lobe. Telson short, broad, hook spines undescribed.

Female (4.6 mm): Rostrum very short, broad, not exceeding lateral head lobes. Antenna 1, peduncular segments more strongly setose; peduncular segment 1 with more pronounced median swelling. Antenna 2, peduncular segments moderately broad; segment 4, posterior margin with 3 pairs of strong spines; segment 5 with stout median spine and several setal clusters; flagellum short, posterior setae short.

Peraeopods 3 & 4, anterior margins of basis and segment 4 relatively sparsely setose. Brood lamellae not described.

Taxonomic and distributional commentary. *Monocorophium uenoi* is apparently endemic to the Sea of Japan and the South China Sea, from whence it has been introduced, in post-W.W. II times, with the importation of Japanese oysters and other fisheries products to San Francisco Bay and other central Californian localities (e.g., Bodega Bay) and southern California (e.g., Newport Bay) (Carleton, 1979; Chapman, 1988). The species has not yet been recorded from the present, more northerly study region.

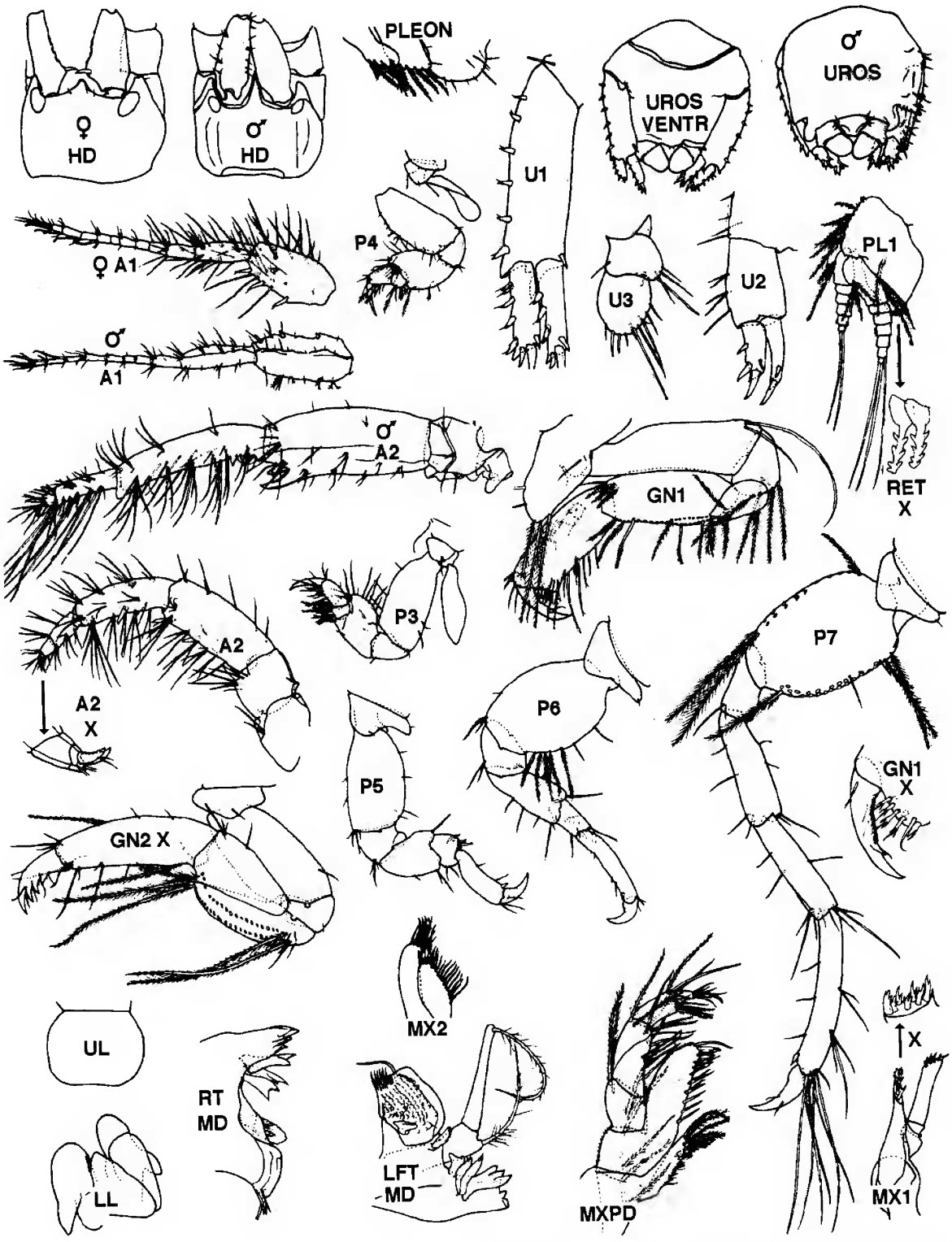

FIG. 31. ***Monocorophium uenoi*** **·(Stephensen). Hong Kong. Male (2.0 mm); female (4.6 mm) (after Hirayama, 1986).**

Monocorophium sextonae (Crawford)
(Fig. 32)

Corophium sextoni Crawford, 1937: 620, figs. 3, 4.

Corophium sextonae Crawford, 1937 emend Hurley, 1954: 433, figs. 1, 2.—Hirayama, 1987b: p. 572, Fig. 3.—Barnard & Karaman, 1991: 185.—Ishimaru, 1994: 35.

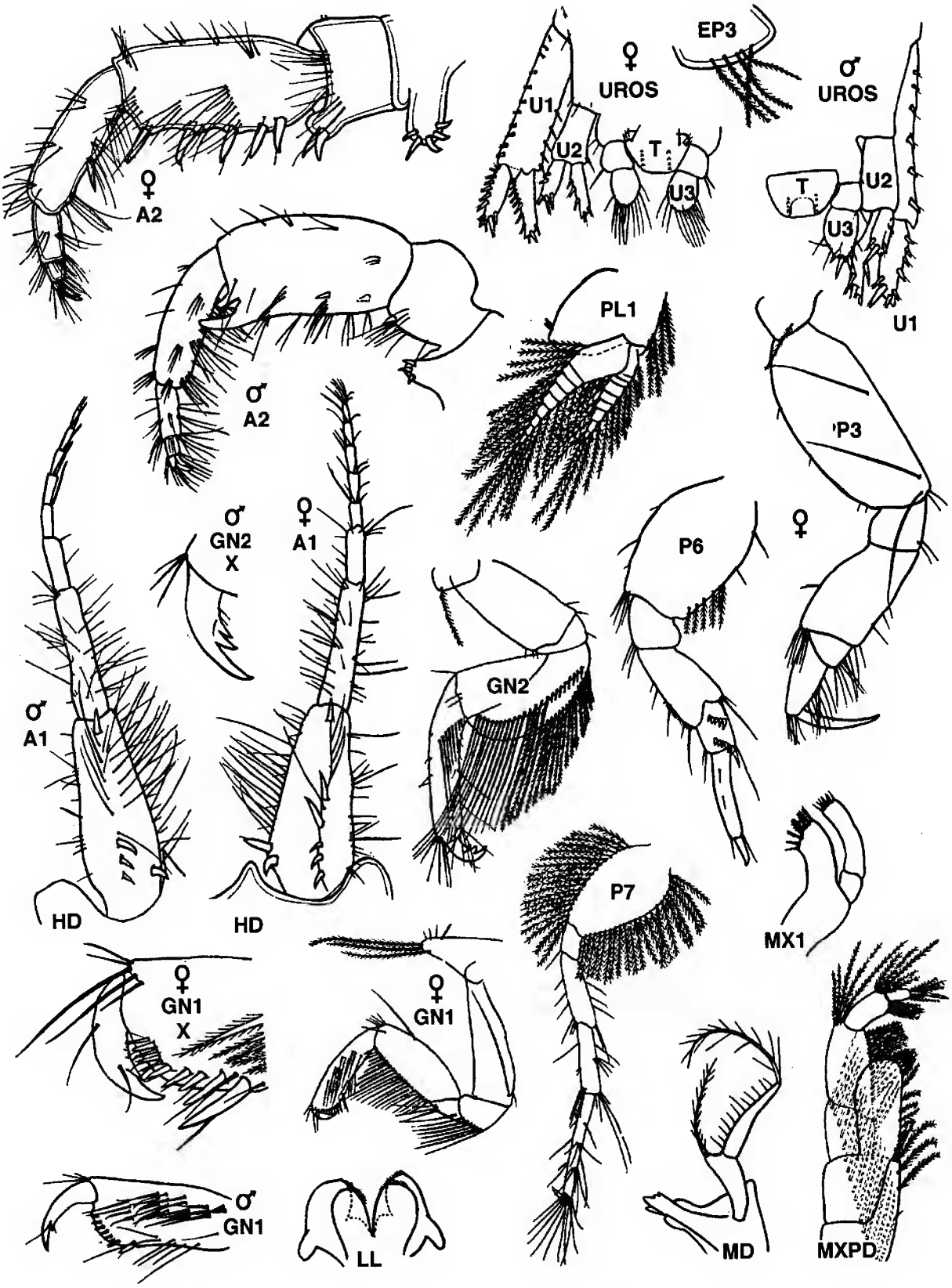

FIG. 32. ***Monocorophium sextonae*** **(Crawford). Otago, New Zealand. Male (4.0 mm); female (5.0 mm) (after Crawford, 1937; Hurley, 1954).**

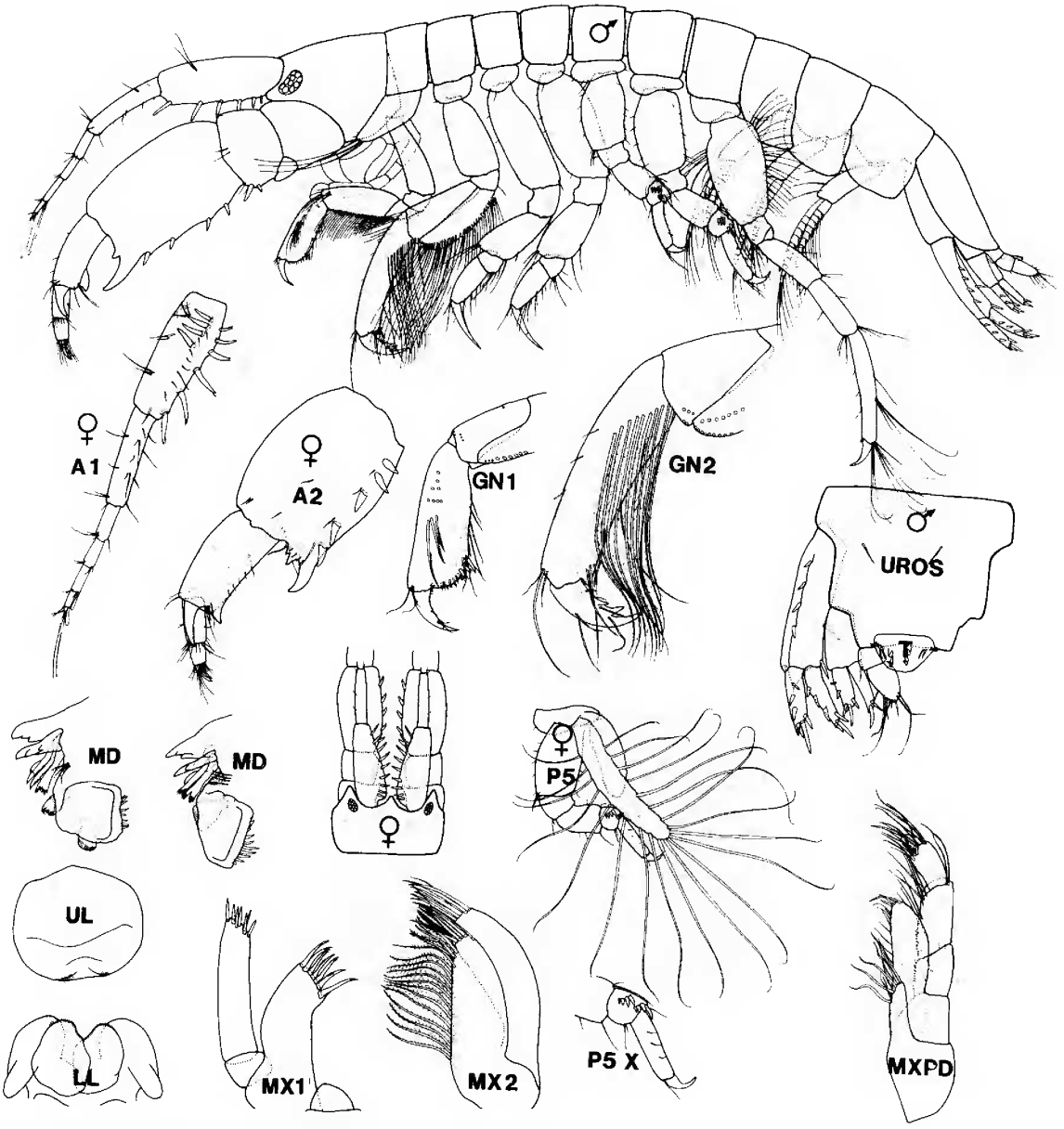

Fig. 32. *Monocorophium californianum* (Shoem.). S. Vancouver I., B.C. Male (3.2 mm); female (2.8 mm).

Taxonomic and distributional commentary.

Monocorophium sextonae is almost certainly endemic to the eastern North Atlantic and Mediterranean regions, from whence it has been spread by commerce to world-wide temperate marine waters, including those of Australia and New Zealand (Hurley, 1954), and the western North Pacific (Nagata, 1965; Ishimaru, 1994). It has not yet been recorded authentically from the eastern North Pacific region. The species exhibits numerous plesiomorphic character states, including a non-sexually dimorphic rostrum, strongly spinose antennae, closed lower margin of the fused merus and carpus, bidentate dactyl of gnathopod 2, and strongly spinose rami of uropods 1 & 2. Some facets of morphological similarity between *Monocorophium sextonae* and *Crassicorophium bonelli* may not be entirely homoplasious.

Monocorophium californianum (Shoemaker)
(Fig. 33)

Corophium californianum Shoemaker, 1934a: 359, fig. 2.—Shoemaker, 1949: 76.—Barnard, 1975: 338 (key).—Otte, 1976: 11, fig. 9.—Austin, 1985: 615.—Barnard & Karaman, 1991: 185.

Material Examined.
BRITISH COLUMBIA .
Southern Vancouver island. Dobrachy Seatech Stn W2B, off McCauley Point, Victoria, August, 1976 - 1 male (3.2mm) (**fig'd**), CMN Cat. No. NMCC1992-0938; ELB Stn P714, 1970 - 1 female ov (2.8 mm), (**fig'd**), CMN Cat. No. NMCC1997-0948.

Diagnosis. Male (3.2 mm): Pleon segment 3 smooth dorsally . Urosome with distinct lateral notches; uropod 1 inserted laterally. Head, rostrum short, broad, tip not exceeding lateral head lobes. Antenna 1, peduncular segment 1 with strong inner marginal and posterior marginal spines; peduncular segment 2 distinctly smaller than 1; segment 3 short, flagellum very short, 4-segmented. Antenna 2 strongly pediform; segment 4 very thick, lower margin with short spines; peduncular segment 5 very short, with large curved distal process and stout posterodistal tooth; flagellum very short, 4-segmented, margins weakly setose.

Gnathopod 1, propod slightly broadening distally, dactyl tip little exceeding palm. Gnathopod 2, basis medium; carpus medium long, with small posterodistal free margin; propod with small posterodistal cusp; dactyl with 2 unequal posterior marginal teeth.

Peraeopods 3 & 4 slightly dissimilar; basis of peraeopod 3 distinctly less broadened than that of peraeopod 4, anterior margins bare; segment 4 little broadened, partly overhanging short segment 5; dactyls slender, slightly longer than segment 6. Peraeopods 5 & 6, hind margin of basis with few setae. Peraeopod 7 not elongate, basis medium; segment 6 with 2 posterodistal clusters of long setae; dactyl short.

Uropod 1, rami short, unequal, each with 3 outer marginal spines. Uropod 2 stout, outer ramus with 2 outer marginal spines, inner ramus bare. Uropod 3, peduncle small, lacking lateral lobe, ramus narrowing distally. Telson short, broad, with 4 posterodorsal pairs of small hook spines.

Female (2.8 mm): Rostrum short. Antennae 1 & 2 similar to those of male but slightly less robust.

Brood lamellae relatively large, strap-like, with few (~20) long marginal setae.

Distributional ecology. Endemic to the North American Pacific coast, from Central California (Monterey Bay) to southern British Columbia, on sandy bottoms to depths of 100 m.

Taxonomic commentary. *Monocorophium californianum* and *M. oaklandense* form a natural subgroup within the genus, distinguished by the very stout, not sexually dimorphic antenna 2, and plesiomorphic condition of the gnathopods (Fig. 41, p. 133).

Monocorophium oaklandense (Shoemaker)
(Fig. 34)

Corophium oaklandense Shoekaker, 1949: 60, fig. 8.—Barnard, 1975: 338 (key), fig. 140.—Otte, 1976:11, fig. 9.—Austin, 1985: 615.—Barnard & Karaman, 1991: 185.

Material examined: None from study region. *Monocorophium oaklandense* is known only from experimental test blocks set out in San Francisco Bay. Otte (loc. cit.) considered this species a possible introduction to coastal waters of British Columbia.

Taxonomic and distributional commentary. *Monocorophium oaklandense* is similar to *M. californianum* in having stout, not sexually dimorphic antennae, and gnathopods of plesiomorphic form. However, the former differs from *M. californianum* in its less spinose, more setose peduncular segment 1, and longer flagellum, of antenna 1; less strongly produced segment 5 of antenna 2; tri-dentate dactyl of gnathopod 2; broader basis of peraeopod 7; marginally spinose inner ramus of uropod 2; and broader ramus of uropod 3.

M. oaklandense is apparently unknown outside the San Francisco Bay region of the Pacific coast of North America. However, it was not recorded in the present more northerly study region.

Apocorophium, new genus
(see Fig. 35)

Corophium Latreille, Crawford, 1937: 623 (Section C+ key).—Shoemaker, 1947: 47 (Section C).—Shoemaker, 1949: 66 (Section C).—Barnard, 1973:17 (part).—Bousfield, 1973:198 (part).—Otte,1976: 4 (part).—Lincoln, 1979: 522 (part).—Myers, 1982: 185 (part).—Barnard & Karaman, 1991: 184 (part).—Ishimaru, 1994: 35 (part).

Type species. *Corophium acutum* Chevreux, 1908 (present designation).

Species. *Apocorophium simile* (Shoemaker, 1934b). *A. lacustre* (Vanhoffen, 1911). *A. louisianum* (Shoemaker, 1934b).

Diagnosis. Urosome segments fused; uropods arising ventrally on urosome. Head, rostrum distinct, interior antennal sinus large, recessed. Antenna 1, peduncular segment 3 short. Antenna 2 short-pediform, sexually unlike (except in *simile*); distal process of segment 4 bidentate; segment 5, median tooth and distal process variously developed; flagellum short, 3-segmented; gland cone short (except in *A. louisianum*).

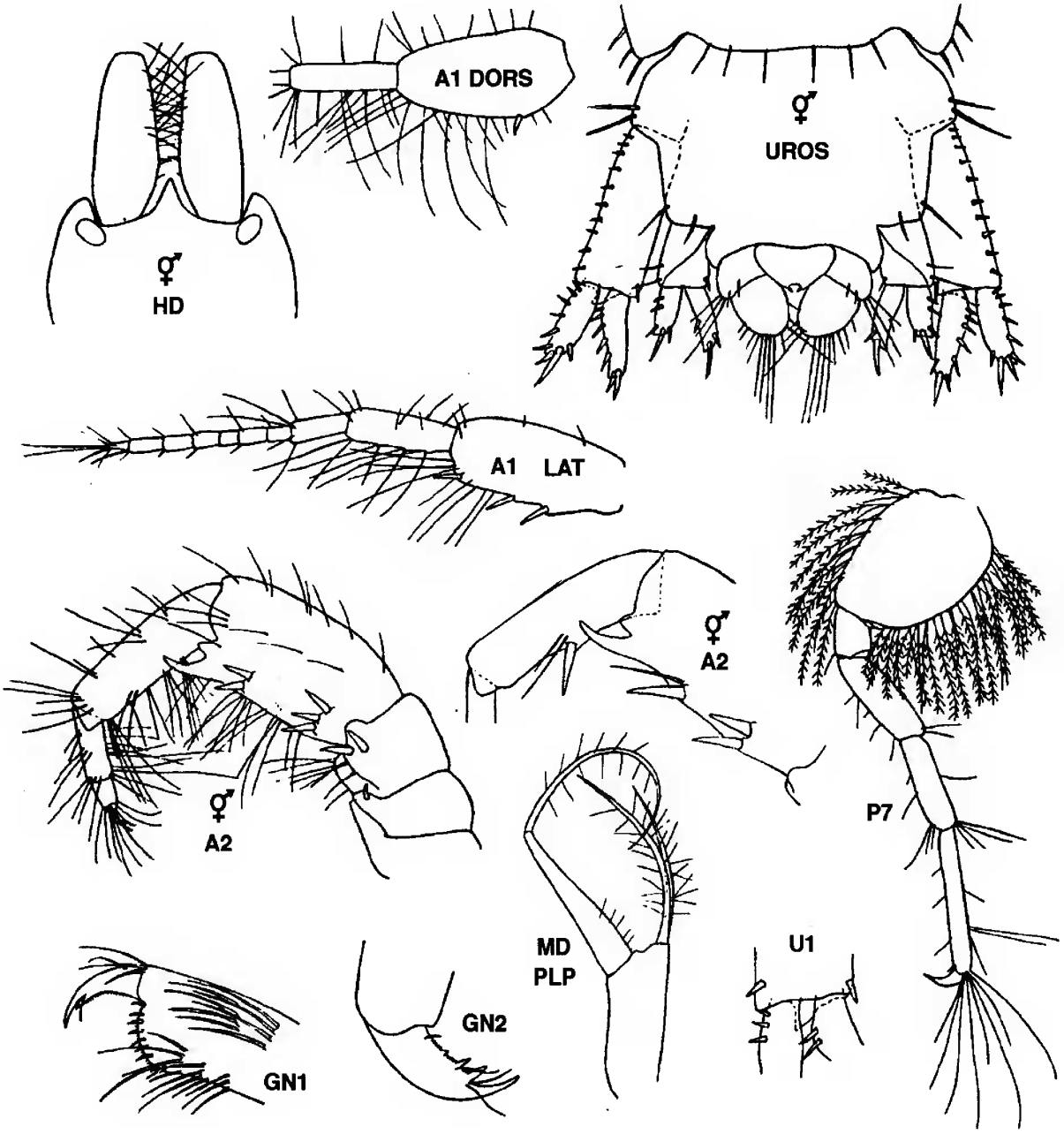

Fig. 34. *Monocorophium oaklandense* (Shoem.). San Fancisco Bay. Hermaphr. ov. (5.0 mm) (after Shoemaker, 1949).

Upper lip, epistome not produced. Lower lip, mandibular lobes strong. Mandibular palp of moderately advanced form (type P4 of Hirayama, 1987b). Maxilla 1, palp short, not exceeding outer plate. Maxilla 2, inner plate slender. Maxilliped, inner plate short; outer plate slender, inner margin setose distally; palp segment 2 short.

Gnathopod 1, dactyl with weak posteriorly marginal tooth, tip little exceeding palm. Gnathopod 2, merus not occluding posterodistal (free) margin of short carpus (~ 1/2 propod); dactyl short, tri- or quadridentate.

Peraeopods 3 & 4, basis broadened, glandular; segment 4 moderately broadened distally, overhanging short segment 5. Peraeopods 5 & 6, segment 4 short; segment 5 short, posterodistal hook spines short, stout; segment 6 and dactyls reversed; basis of peraeopod 6, hind margin setose. Peraeopod 7 not markedly elongate; dactyl short.

Pleon plate 3, hind corner obtuse or rounded. Pleopod peduncles very broad distally. Uropods 1 & 2, peduncles stout, broad; rami short, subequal, spinose on outer margin and apically, apex acute, curved outwards. Uropod 3, ramus short, broad, apex rounded, setose. Telson regular, with dorsal hook spines, apex rounded.

REVISED KEY TO SPECIES OF *APOCOROPHIUM*

1. Antenna 2 essentially similar in male and female ..... *A. simile* (Shoem.)
—Sexes more or less unlike ..... 2.

2. Antenna 2 (male), segment 5 with strong medial tooth ..... *A. acutum* (Chevreux).
—Antenna 2 (male) lacking medial process ..... 3.

3. Antenna 1 (male), peduncle 1 strongly setose anteriorly, with no basal process .. *A. lacustre* (Vanhoffen)
—Antenna 1 (male), peduncle 1 weakly setose but strong basal process ..... *A. louisianum* (Shoemaker)

Coxal gills slender, sac-like, on peraeopods 3-6, small on peraeopod 6. Brood lamellae short, slender, margins regularly setose.

Etymology. Combining the Greek prefix "*apo*" - advanced, and the generic root "*Corophium*", with reference to the overall apomorphic character states of member species.

Distributional ecology: Small to medium-sized species living in open-ended abodes, usually colonial, cemented to hydroids, wharf piling, oysters, and other solid substrata. Occurring mainly in coastal summer-warm marine and brackish waters of the Atlantic and Mediterranean regions; widely synanthropic in the western North Pacific and the Southern Hemisphere, including Australia and New Zealand (Hurley, 1954).

Taxonomic commentary. Crawford (loc. cit.) first recognized and keyed this group as a distinct taxonomic assemblage. However, neither he nor Shoemaker (1947, 1949) gave it formal taxonomic recognition. The genus *Apocorophium* may be a polymorphic assemblage of two or three separate lineages. Thus, the type species *A. acutum* has evolved from Atlantic regional ancestors (*Monocorophium* subgroup) in concert with, but differing from, other Atlantic apocorophiids in having strongly sexually dimorphic antenna 2, with medially and distally processiferous peduncular segment 5.

The Pacific species, *Corophium baconi*, superficially seems to belong here. It differs in having a processiferous epistome on the upper lip, more advanced mandibular palp (Type P5 of Hirayama, 1987), bidentate dactyl of gnathopod 2, laterally notched urosome, much reduced uropod 2, strongly lobate peduncle of uropod 3, and may have evolved independently from a Pacific-endemic ancestral form (below).

Laticorophium, new genus

Corophium Latreille 1806, Shoemaker, 1934a: 356 (part).—Crawford, 1937: 623 (Section C, part).– Shoemaker, 1949: 66 (Section C, part).—Otte, 1976: 2 (+ key, part).—Hirayama, 1986: 449 (part).—Barnard & Karaman, 1991: 184 (part).—Ishimaru, 1991: 35 (part).

Type species. *Corophium baconi* Shoemaker, 1934a (monotypy).

Diagnosis. Urosome segments fused, lateral margins notched. Uropods inserted ventrally. Head, rostrum short, little sexually dimorphic; inferior antennal sinus strongly regressed. Antenna 1, peduncular segments 1 & 2 long, 3 short. Antenna 2 markedly sexually dimorphic, strongly pediform (male); gland cone short; peduncular segment 4, posterodistal process bifid; segment 5 with strong medial and distal processes; flagellum short, with apical spines.

Upper lip, epistome produced anteriorly. Lower lip, mandibular lobes medium. Mandibular palp, basal segment with notched shelf (type P4 of Hirayama, 1987b); blades few (2-3), stout. Maxilla 1, palp slender, slightly exceeding outer plate. Maxilliped, inner and outer plates short; palp segment 2 short.

Gnathopod 1, dactyl bifid, tip exceeding short, oblique palm.. Gnathopod 2, carpus short, deep, posterodistal setose free margin not occluded by short merus; propod lacking palm; dactyl short, typically bidentate.

Peraeopods 3 & 4 short; basis broad, glandular; segment 4 broadened distally, slightly overhanging short segment 5. Peraeopods 5 & 6 short, similar in form but bases markedly unequal in size; segment 5 short, with 2 posterolateral clusters of short hook spines; segment 6 and dactyl reversed. Peraeopod 7 not elongate; basis medium broad; dactyl short.

Pleon plate 3, hind corner rounded. Pleopod bases strongly broader than deep, proximo-medial margin strongly convex; rami short. Uropod 1, peduncle stout, outer ramus the shorter, outer margins spinose, apices acute, curved outwards. Uropod 2 relatively small, outer margin of rami setose. Uropod 3; peduncle with distinct lateral lobe; ramus short, broad, subtriangular. Telson not broader than long, apex rounded.

Coxal gills narrow, sac-like, on peraeopods 3-6. Brood lamellae linear, margins moderately setose (<20), on peraeopods 3-5.

Etymology. A combining form of the Latin prefix "latus" - broad, and the generic root *Corophium,* with reference to the very broad, short urosome.

Distributional ecology. Endemic to the North American Pacific coast; probably synanthropic in the Sea of Japan.

Taxonomic commentary. Crawford (1937) placed *Corophium baconi* in Section C, which contained *Corophium acutum* and related species having urosome segments

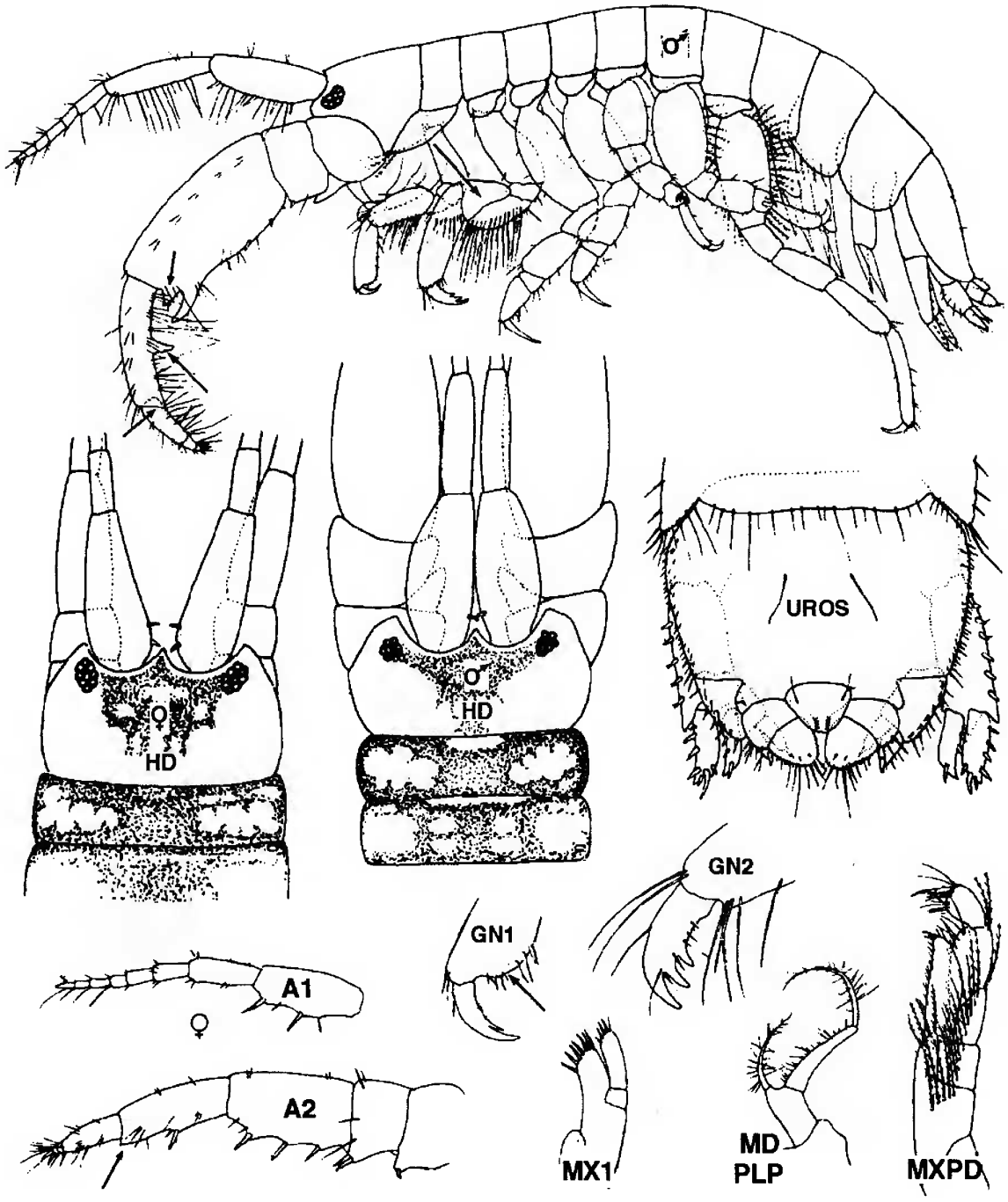

FIG. 35. *Apocorophium acutum* (Chevreux). Woods Hole region. Male 2.3 mm); female (2.0 mm) (after Bousfield, 1973).

fused, and uropods arising ventrally. This decision was accepted by Shoemaker (1949), Otte (1976), and Hirayama (1986). However, as noted above and in the phenogram (Fig. 40, p. 133), *L. baconi* is generically distinctive in its strongly processiferous epistome of the upper lip, the columnar form of the maxillipedal outer plate, the bidentate dactyl of gnathopod 2, and the short broad, laterally notched urosome.

Laticorophium baconi (Shoemaker)
(Figs. 36, 37)

Corophium baconi Shoemaker, 1934a: 356-359, fig. 1.—Shoemaker, 1949: 82, fig. 5g, h.—Barnard, 1970: 101, fig. 53.—Otte, 1976: 11, fig. 8.—Hirayama, 1986: 472, figs. 12-14.—Barnard & Karaman, 1991: 185.—Ishimaru, 1994: 35.

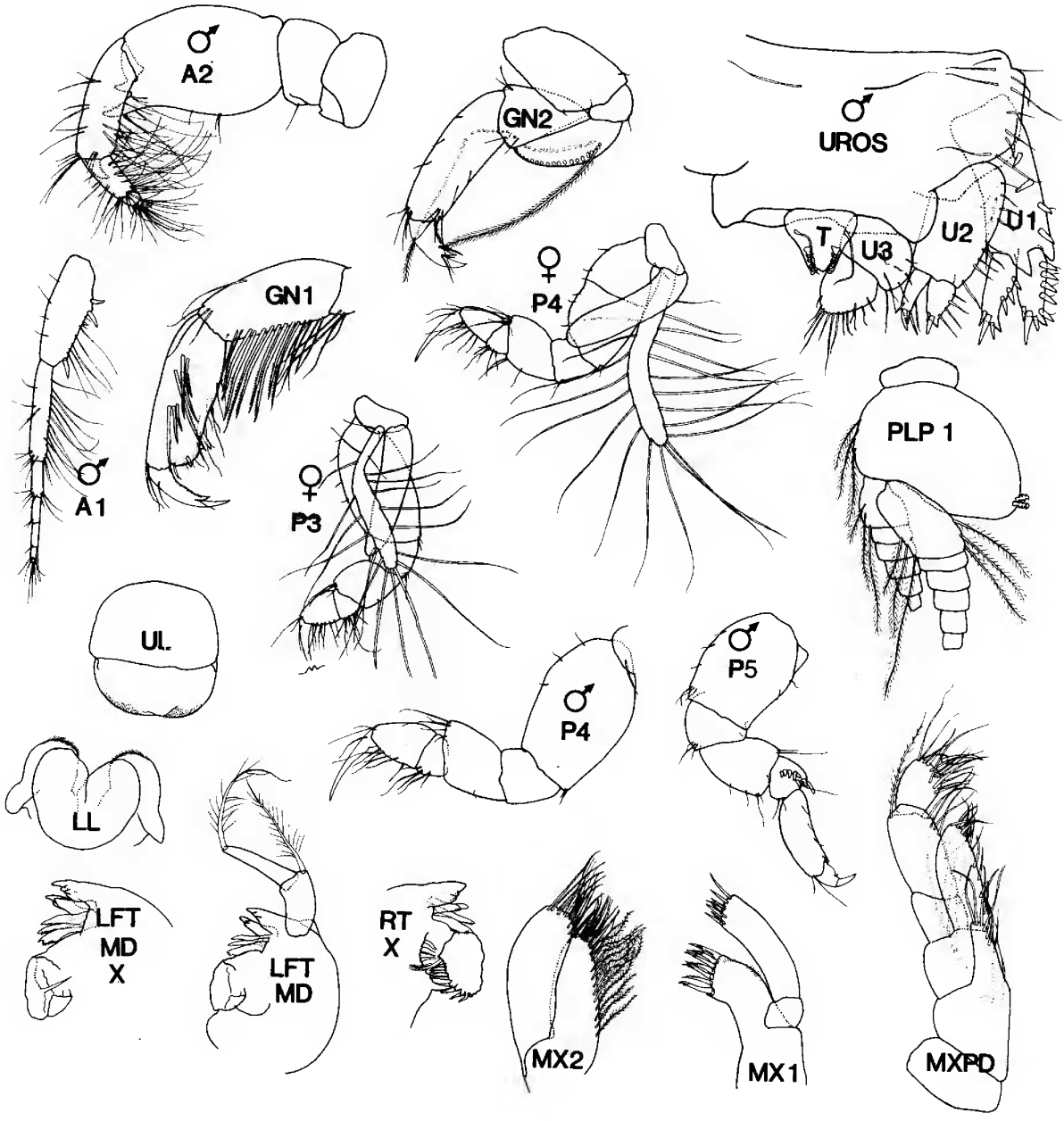

FIG. 36. ***Laticorophium baconi*** **(Shoem.). Goose I., B. C. Male (4.0 mm). Pidwell Reef, B. C. Female 4.0 mm).**

Material Examined. 36 specimens in 15 lots, as follows:
ALASKA.
Aleutian Islands. Unimak I., N. A. Powell, Stn, IzeMbek lagoon., 1969 - 2 males, 4 imm (damaged).

BRITISH COLUMBIA.
Queen Charlotte Islands. FRB survey, JWS Stn 106 (Hecate Strait), 1965 -1 im.
North-central mainland coast. ELB Stns, 1964. H34 (Pidwell Reef) - 1 female (**fig'd** spmn), CMN Cat. No. NMCC1942-0948.(3), H50 (Goose I. anchorage) - male (4.0 mm) (**fig'd** spmn), 1 male, 1 female, CMN Cat. No. NMCC1992-0872.
Vancouver Island. North end. ELB Stn B29a (Gooding Cove), 1975 - 2 females.
South end and southeastern mainland coast. ELB Stn H44 (off Brady's Beach), 1964 - 1 female; ELB Stns, 1970: P714 (7), P719(4); ELB Stn, 1975: P14(1); ELB Stn, 1976, EB2 (Burrard Inlet) - 2 im; ELB Stns, 1977: B16(2), B19b(1), B21b(1); ELB. Stn, 1978, V6 (Burrard Inlet) - 1 female.

WASHINGTON.
Juan de Fuca Strait. ELB Stn, 1966: W35(1).

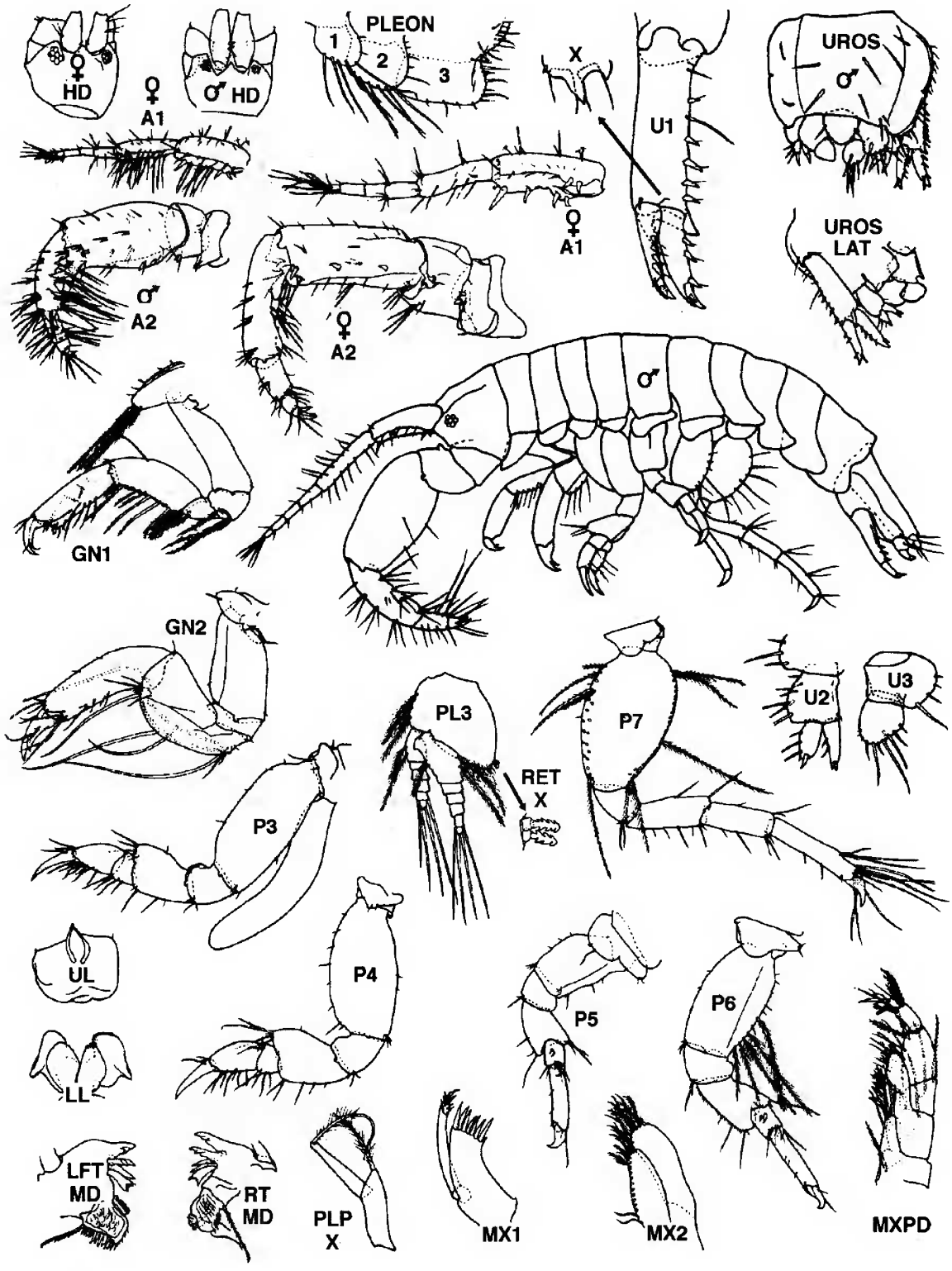

FIG. 37. *Laticorophium baconi* (Shoem.). Hong Kong. Male (3.4 mm); female (3.2 mm) (after Hirayama, 1986).

Diagnosis. Male (3.4 mm): Pleosome segment 3 with slight posterior marginal elevation. Urosome short, broad, with convex lateral margin, entire except for slight notch posterior to ventral insertion of uropod 1. Head, rostrum short, basally broad, tip not exceeding lateral head lobes. Antenna 1 slender; peduncular segment 1 with 2 proximo-

medial and 3-4 posterior marginal spines; segments 1 & 2 strongly setose posteriorly; segment 3 short; flagellum 3-segmented. Antenna 2 short, strongly pediform; segment 4 deep, nearly smooth below; peduncular segment 5 shorter than 4, with distinct distal median tooth and strong curved distal process; flagellum medium, 3-segmented; posterior margin of segment 5 and flagellum strongly setose.

Gnathopod 1, propod margins subparallel; dactyl with small posterior marginal tooth, tip distinctly exceeding short palm. Gnathopod 2, basis stout; carpus short, with distinct posterodistal free margin; propod strong, lacking palm or posterodistal cusp; dactyl with a single posterior marginal tooth and a few setae.

Peraeopods 3 & 4, bases broad (3 slightly narrower than 4), anterior margin nearly bare; segment 4 distally medium broad, strongly overhanging short segment 5, anterior margin (of 4) nearly bare; dactyl slender, subequal in length to segment 6. Peraeopod 5, posterior margin of basis nearly bare. Peraeopod 7 not elongate; basis medium broad; segment 6 with 2 distal clusters of long setae; dactyl short.

Pleon plates 1 & 2 with long marginal setae; pleon plate 3 setose behind. Uropod 1, rami short, unequal, each with 2-4 outer marginal spines. Uropod 2 small; outer ramus with 3-4, and inner ramus with 1-2, slender outer marginal spines. Uropod 3, peduncle broad, with distinct setose lateral lobe; ramus short, narrowing and rounded apically. Telson little broader than long, narrowing distally, with 4 posterodorsal pairs of small hook spines.

Female (3.2 mm): Rostrum and antenna 1 much as in male. Antenna 2 dissimilar to that of male; peduncular segments 3 & 4 with short posterior marginal spines; segment 5 shorter than 4, margins weakly setose; margin of segment 5 with 3 pairs of strong spines; flagellum short, with medium setae.

Brood lamellae relatively short and slender, with few (~20) marginal setae.

Taxonomic and distributional commentary. Specimens from the North American Pacific region (Fig. 36) differ little from those of the Asiatic North Pacific region (Fig. 37), confirming the high probability that the latter are synanthropic in the western Pacific. However, as the writers did not examine material of the latter, further study is recommended.

Laticorophium baconi is unlike all other North American Pacific corophiins in its unique combination of plesiomorphic and apomorphic character states. (Fig. 40, p. 133). Plesiomorphic character states include the processiferous epistome and weakly toothed form of the dactyl of gnathopod 2. Advanced character states include the form of the mandibular palp (type P5), short maxillipedal palp segment 2, and ventral insertion of uropod 1. Although the phenetic similarity of *L. baconi* is closest to the advanced *Monocorophium-Apocorophium* North Atlantic complex of species (Fig. 40, p. 133), its phyletic affinities may lie with the more primitive arctic and western North Pacific genera (viz, *Crassicorophium* and *Hirayamia* respectively).

DISCUSSION AND CONCLUSIONS

The genus *Corophium* Latreille sens. lat. has long posed a difficult taxonomic and classificatory problem within superfamily Corophioidea. Considerable morphological diversity is encompassed within the 60+ species previously assigned to this generic concept. Such diversity exceeds tolerable species group limits within almost any other gammaridean amphipod species complex of comparable size, as well as some less speciose generic groups. For instance, fusion of urosome segments is elsewhere considered a character state of significance at the family level (e.g., Kuriidae, Thaumatelsonidae) or even in superfamily classification (e.g., Ampeliscoidea) (Barnard, 1969a; Barnard & Karman, 1991).

The present study of North American Pacific corophiins treats barely 20% of the known world species, and only one that is new to science. However, in attempting to deal realistically with the systematics of even this relatively limited but diverse assemblage of species, the need for critical assessment of character states other than those previously employed (e.g., form of the rostrum, antennae and urosome) became apparent. Hirayama (1987b) had proposed hypothetical phylogenies based on the form of the mandibular palp (where described), and proposed new categories of urosome and uropod arrangement based on newly discovered Asiatic North Pacific taxa. However, as detailed in the systematic section (above), morphological correlations of potential generic significance soon became apparent in most other appendages. These included the structure of the gnathopods, especially the armature of the dactyls and degree of fusion of merus and carpus of gnathopod 2, the shortening and broadening of segments of peraeopods 3-6 (associated with development of silk glands and "spinning" apparatus), broadening of pleopod peduncles, and modifications of uropods 1-3.

The present revision has also been greatly aided by a series of revisionary studies on the sister corophiid subfamily Siphonoecetinae, by Jean Just (1983, 1984, 1988). His classification is essentially phyletic and reflects apparent changes in life style from free-burrowing (primitive) to abode-building (advanced). However, unlike siphonoecetins, free-burrowing corophiins occur mainly on pure sediments with little macro-particulate detritus. Furthermore, domicolous corophiins live mainly in fixed abodes on hard substrata, or on shell-modified soft substrata, usually in large colonies. If animals relocate elsewhere, they cannot transport the abode with them but must crawl or swim freely to a new location, and there construct a new abode, or evict another tenant from an existing tube (Shillaker & Moore, 1983, etc.?). As in the Siphonoecetinae, however, increasing adaptation within the Corophiinae from a burrowing to a domicolous life style is reflected in corresponding morphological changes. Thus, peraeopods apparently become less fossorial and/or ambulatory but more specialized for secretion of cementing silk and/or clinging to the tube walls. Moreover, in various ways the

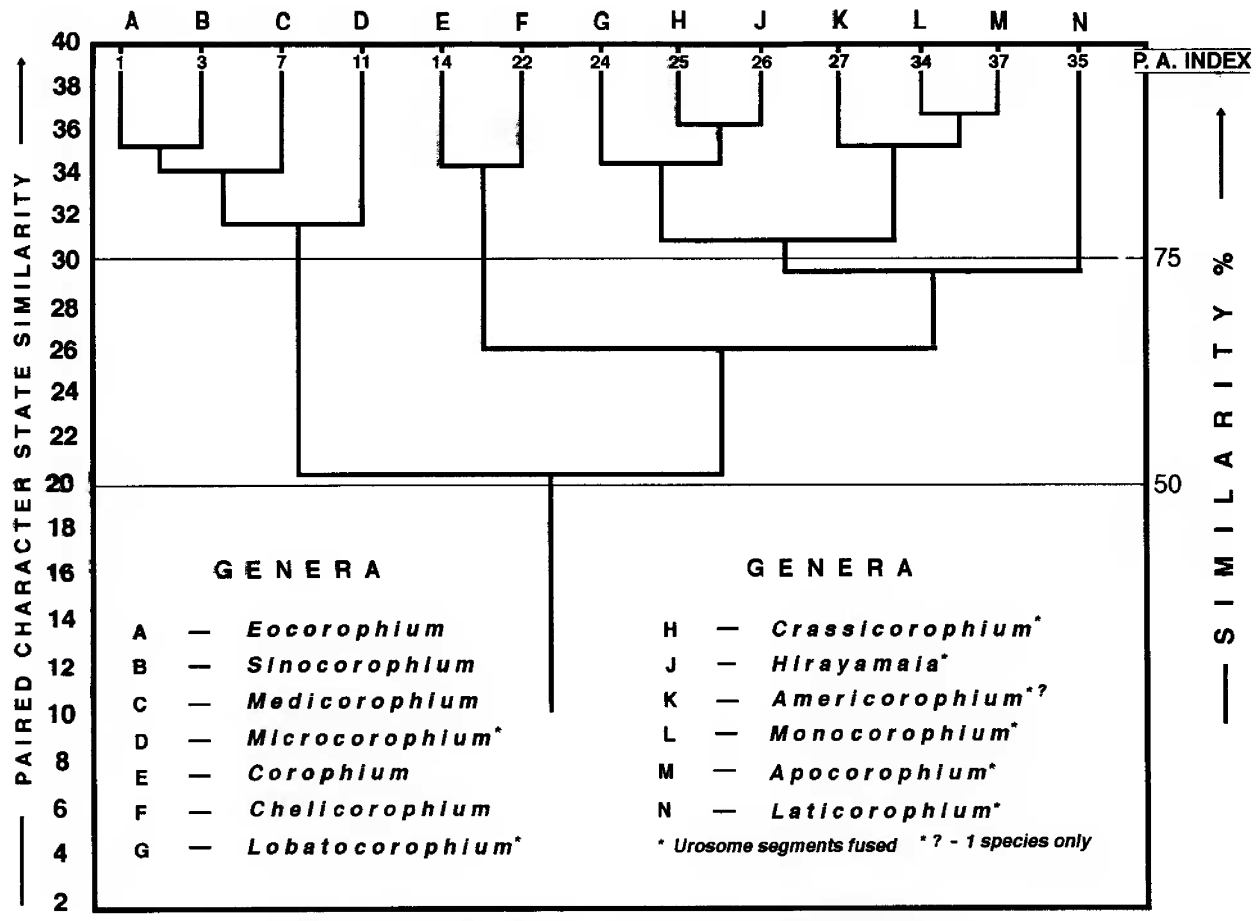

FIG. 38. PHENOGRAM: GENERA OF COROPHIINAE

urosome becomes more efficiently modified for "plugging" the rear entrance of the tube when the animal is active at the other end. Facilitating the corophiin "fixed" life style, the double opening of the abode presumably permits the animal to continuously filter food particles borne by directionally changing tidal currents.

The distant ancestry of corophiin amphipods is undoubtedly shared with most other members of family Isaeidae. However, their direct ancestry is more problematical. The genus *Corophium* sens. lat. (= subfamily Corophiinae) has been widely considered a monophyletic concept because of the unique form of the mandibular palp, the filtering apparatus of the gnathopods and other autapomorphies of all member species. They are also closer to siphonoecetins than to other potential isaeid outgroups because of many shared synapomorphies, several of which are outlined by Just (1983). Common features include: lack of accessory flagellum; pediform antenna 2; basically 2-segmented mandibular palp; lack of gill plate on peraeopod 2; small separated coxal plates 1-4; and dissimilar gnathopods 1 & 2.

Generic relationships within subfamily Corophiinae

Morphological similarities of corophiin genera are indicated by the phenetic analysis summarized in Fig. 38 (above). Corresponding characters and character states of the cluster analysis are provided in Table I (p. 131).

Three main subgroupings may be considered here: (1) A cluster of 4 primitive genera to the left (P. A. Indices of 1-11) that differs from the other subgroupings at the 50% similarity level; (2) a cluster of 7 advanced genera to the right (P. A. Indices of 24-35); and (3) a cluster pair of intermediate genera in the centre-left (P. A. Indices of 14-22) that differs from the advanced cluster at the 65% similarity level.

With respect to (1), character states of mouthparts, gnathopods, peraeopods and uropods are unspecialized and plesiomorphic. Only in *Microcorophium* are urosome segments fused. Three genera are endemic to the Asiatic North Pacific, one genus (*Medicorophium*) to the Mediterranean region, and one species of *Sinocorophium* (*S. alienense*) is considered synanthropic in the eastern North Pacific.

Within cluster (2) are three subclusters, viz: on the left, a relatively primitive subgroup of *Lobatocorophium, Crassicorophium,* and *Harayamaia*, each with autapomorphic features, but having gnathopod 2 plesiomorphic in form. On the centre right are 2 speciose genera, with variously advanced character states, especially of the gnathopods and peraeopods 4-6, and of probable close common ancestry. Member species are presumably the most specialized in construction of cemented abodes, and in mate-guarding reproductive behaviour. The condition of the urosome and appendages grades from the generally unfused condition in *Americorophium,* through fusion and various degrees of ventral inser-

TABLE I. CHARACTERS & CHARACTER STATES OF GENERA OF COROPHIINAE

CHARACTERS	CHARACTER STATE		
	Plesiomorphic 0	**Intermediate 1**	**Apomorphic 2**
1. Inferior antennal process	Produced	Vertical	Regressed
2. Antenna 1 (female), peduncle 1 , posterior spines	None	1 - 2	3+
3. Antenna 2 (male), peduncle 2 , gland cone	elongate, acute	medium	very short
4. A2, peduncle 4, posterodistal process	single tooth		double tooth
5. A2, peduncle 5, proximal posterior tooth	lacking	small	strong
6. Antenna 2 (female), peduncle 4, marginal spines	none	2-3 spines	4+ spines
7. Antenna 2 (female)	sim. to male; ped. 4 process simple	sim. to male; ped. 4 process bifid	hermaphroditic; simple reduced process
8. Mandibular palp	segment 3 continuous with fused segments 1 & 2	segment 3 angled inner seta on flat shelf	segment 3 oblique setal process strong
9. Lower lip, mandibular lobes	weak		distinct
10. Maxilliped, palp segment 2	Elongate; L ~=2X segment 1		Short; L ~= segment 1
11. Gnathopod 1; form of subhela	palm vertical, dactyl short		palm oblique, dactyl well exceeding palm
12. Gnathopod 2; form of dactyl	simple	1-2 posterior teeth	3-5+ posterior teeth
13. Peraeopods 3 & 4; segment 4	slender	slightly broadened	stout, distally broad
14. Peraeopods 3 & 4; segment 5	slender, normal		very short, overhung by segment 4
15. Peraeopod 6, segment 5	length subequal to segment 4		very short << seg. 4
16. Peraeopod 6, segment 5 posterodistal spines	elongate, => 1/2 segment 5		very short, <1/4 segment 5
17. Peraeopod 7, segment 4	Elongate; L ~=Basis	Medium; L~=3/4 Basis	Short; L = 1/2 Basis
18. Pleon plate 3, hind corner	Acute, produced	Squared	Rounded
19. Urosome	Segments separate, uropods 1 & 2 inserted laterally	Segments 1-3 fused uropods inserted laterally	Segments 1-3 fused uropod 1 inserted ventrally

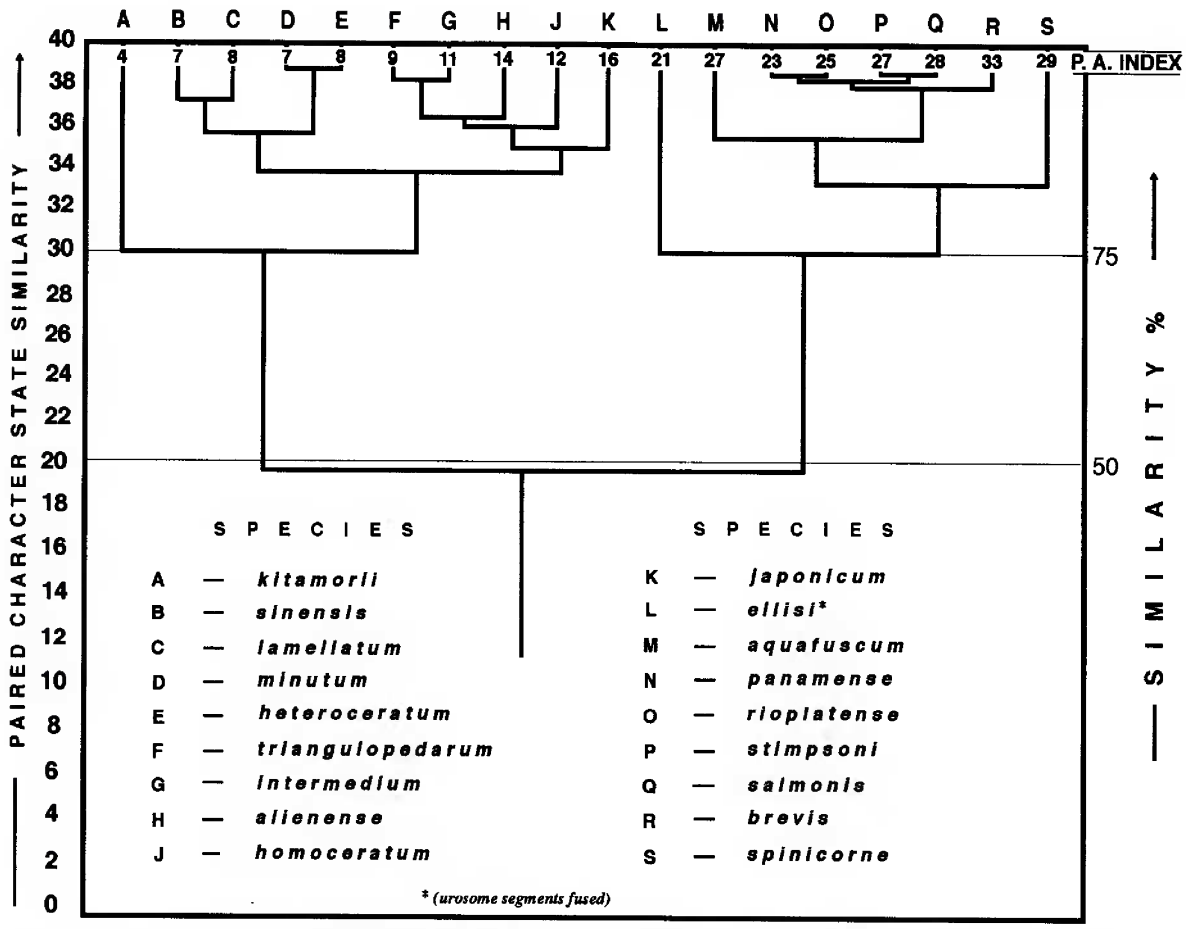

FIG. 39. PHENOGRAM: NORTH PACIFIC AND NEOTROPICAL SPECIES OF COROPHIINAE HAVING UROSOME SEGMENTS UNFUSED.

tion of uropod 1 within *Monocorophium*, to the fully fused, and fully ventral insertion of uropod 1 in *Apocorophium*. On the extreme right is the monotypic, North Pacific genus *Laticorophium*, having similarly advanced character states but plesiomorphic gnathopods and probably of differing close ancestry. The centre-left generic pair of *Corophium* and *Chelicorophium* (3) encompasses mostly littoral, mainly burrowing species, having unfused urosome segments and plesiomorphic mouthparts, but exhibiting variously advanced condition of antennae, gnathopod 2, peraeopods and uropods.

The species groupings of Crawford (1937) and Shoemaker (1947, 1949), based on the degree of fusion of urosomal segments and ventral insertion of uropod 1, are generally supported at generic level in this analysis. Differences are attributable to relatively recent discoveries of several new morphotypes, especially in the Asiatic Pacific region, and by the classificatory significance attributed to other character states by Hirayama (1987b) and the present authors.

Analysis of North Pacific corophiins with unfused urosomes.

The phenogram of corophiins with unfused urosomes (Fig. 39. p. 133) reveals two main subgroupings: (1) a complex of several primitive, largely Asiatic North Pacific species on the left (P.-A. indices of 4-16), and (2) an assemblage of relatively advanced, largely North American Pacific species on the right (P.-A. Indices of 21-33).

With respect to (1), *kitamori* is isolated from the other nine species at the 75% level, and is placed within its own genus, *Eocorophium;* the others are encompassed within *Sinocorophium*, new genus. Species of *Sinocorophium* cluster into two closely similar species subgroups, viz., a primitive complex of 4 sexually dimorphic species to the left, including the generic type species *S. sinensis* (Zhang), and a more advanced subgroup of 5 non sexually dimorphic species to the right. As noted above, the Mediterranean-endemic genus *Medicorophium* is more closely similar to the former, and the western European nominate genus *Corophium* more probably had a common ancestor with the latter.

A subgrouping of species within the relatively advanced complex (2) occurs at comparable similarity levels. Thus, the large western Atlantic estuarine species *Americorophium ellisi* (to the left) is somewhat isolated from other neotropical and eastern Pacific congeners to the right, both in plesiomorphic features (e.g., 3-segmented mandibular palp and simple, posteriorly setose dactyl of gnathopod 2), and apomorphic character states (fused urosome segments; shortened processiferous antenna 1). Within the advanced

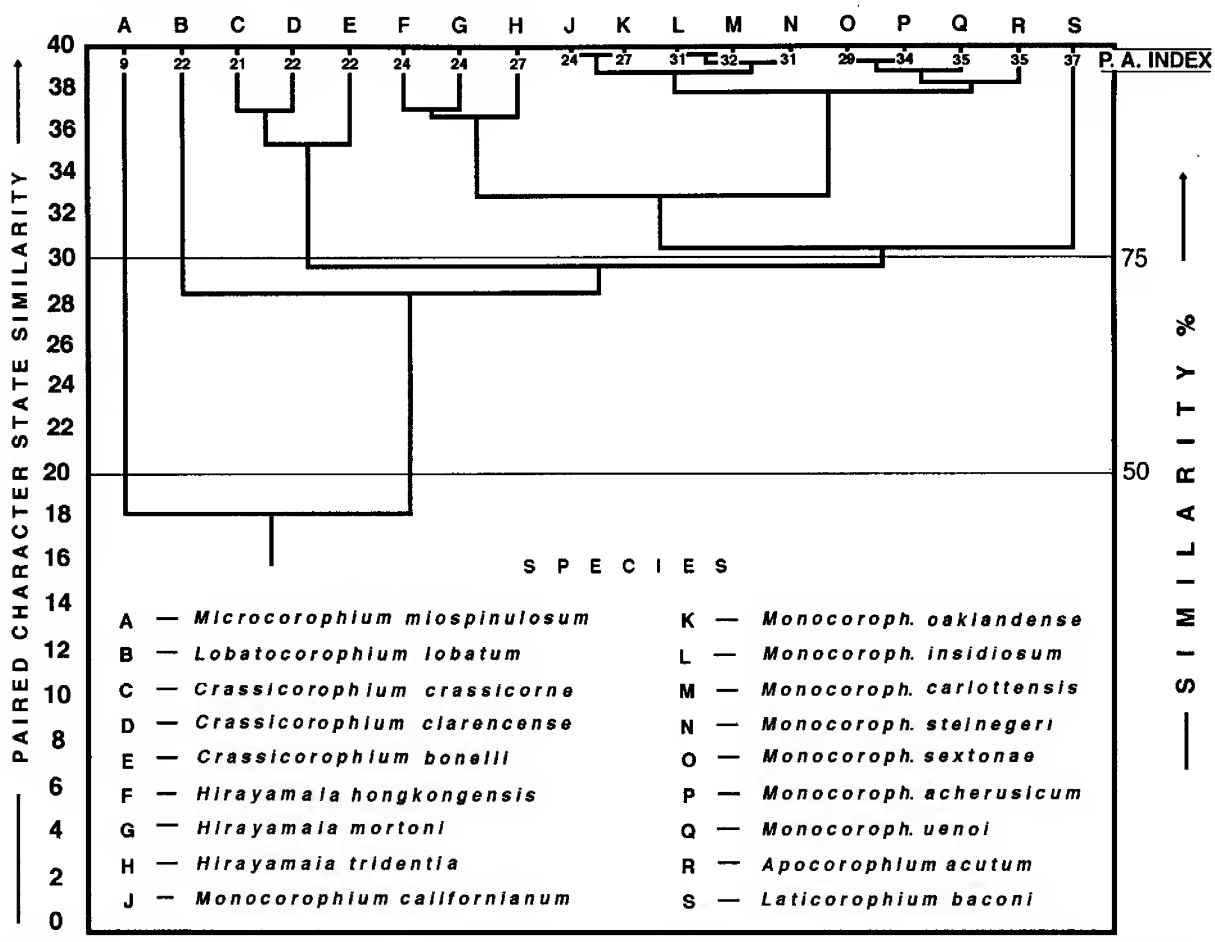

FIG. 40. PHENOGRAM: NORTH PACIFIC SPECIES OF COROPHIINAE HAVING UROSOME SEGMENTS FUSED (COALESCED).

Americorophium subgrouping to the right, three of the Pacific species cluster closely with the other sexually dimorphic Panamanian and Argentinian species. The Pacific species, *A. spinicorne*, and the Atlantic species, *A. aquafuscum*, are similar to each other in having heavily setose, not sexually dimorphic antenna 2, and several plesiomorphic features including a 3-segmented mandibular palp in *A. aquafuscum*. Such internal disparity of higher level character states might justify further generic subdivision, especially in the case of *A. ellisi*. However, more complete description of the mouthparts, coxal gills, brood lamellae, pleopods and other character states, not treated in the original description, is first recommended. The tropical North American Pacific species, *A. setosum* Shoemaker, 1949, appears most closely similar to *A. panamense* in character states described to date. However, the original account did not treat mouthparts and several other analytically critical taxonomic features, so the species has been omitted from the present analysis.

Analysis of North Pacific corophiins with fused urosome.

Three major subgroupings are revealed in the pertinent phgenogram (Fig. 40, above): (1) A primitive monotypic genus *Microcorophium* on the extreme left (P.A. Index of 9); (2) three advanced and closely similar subgroups on the right (P.-A. Indices of 29 to 37)(at and below the 75% similarity level); and (3) three intermediate subgroups on the centre left (P.-A. Indices of 21 - 27).

With respect to (1), in nearly all major character states, *Microcorophium miospinulosum* is remote from other North Pacific subgroups having fused urosomal segments (<50% morphological similarity), but is most closely similar to the primitive western North Pacific genus *Sinocorophium* (Fig. 38) that has unfused urosomal segments. Such a morphological anomaly suggests that fusion of urosome segments may be a convergent feature and therefore not reliable as a primary cladistic character state within the Corophiinae.

Within the intermediate subgroup (3), *Lobatocorophium* is distinctive in the unique form of its urosomal "plug". The genus is most closely similar to the similarly western Pacific-endemic genus *Hirayamaia* (below). The genus *Crassicorophium* encompasses three arctic and subarctic species that demonstrate generally intermediate character states and a trend to intersexual and parthenogenetic reproduction. The most advanced species, *C. bonelli*, may merit separate subgeneric recognition. The genus *Hirayamaia* embraces three western Pacific species, slightly more closely similar in generic-level character states, particularly in the partly ventral insertion of uropod 1. *H. tridentia* may prove sub-

generically distinctive in its relatively advanced form of peduncular segment 5 of antenna 2, and propod and dactyl of gnathopod 2.

In the morphologically most advanced major subgroup (2) uropod 1 arises partially to fully ventrally on the fused urosome. The genus *Monocorophium* encompasses several closely similar species in which uropod 1 arises mainly laterally. These may be clustered within 3 further subgroups: a *californianum-oaklandense* pair on the left, having sexually similar antenna 2 and plesiomorphic form of gnathopod 1; a largely North Pacific endemic *insidiosum-carlottensis-steinegeri* complex in the centre, and an *acherusicum-sextonae-uenoi* assemblage on the right. The latter overlaps morphologically with members of the genus *Apocorophium* in which uropod 1 arises fully ventrally on the urosome. On the extreme right is the distinctive, monotypic North Pacific genus *Laticorophium.* As noted above (p.125), the latter shows mostly advanced character states, but also relatively plesiomorphic features of the antennal gland cone, mandibular palp, gnathopod 2, and a unique notching of the urosome lateral margin.

Systematics of other corophioidean subgroups.

Other corophioideans with superficially similar cylindrical body form and possible close common ancestors to corophiins, previously assigned to family Corophiidae by Bousfield (1982), also listed by Just (1983), include: (1) *Janice* Griffiths, 1976, and *Ritaumius* Ledoyer, 1978b. However, these genera have an elongate antenna 1 with accessory flagellum; sternal processes; subequal gnathopods (gnathopod 1 slightly dominant), and peraeopods 5-7 subsimilar in form; (2) *Kamaka* Derzhavin, 1923 and *Gaviota* Barnard, 1962 *(=Ampelisciphotis* Pirlot, 1938). However, both genera exhibit isaeid synapomorphies that rule out direct ancestry to corophiins, as well as to siphonoecetins.

On the other hand, a few antiboreal and tropical isaeid genera embrace character states that appear, at least superficially, corophiin or ancestrally corophiin in form. Such features include an elongate, lobate, and setose merus of dominant gnathopod 2. The three genera, *Paracorophium* Stebbing, 1899, *Chaetocorophium* Karaman, 1979b, and *Stenocorophium* Karaman, 1979, have been assigned to family Corophiidae by most previous authors (e.g., Barnard, 1969a, Karaman, 1979a). However, because their combination of defining character states includes an elongate antenna 1, basically 3-segmented mandibular palp; deep overlapping coxal plates; fused urosome segments 1 & 2; and primarily biramous uropod 3, none can be directly ancestral to corophiins, or (more improbably) to the sister-group siphonoecetins. In our view, those genera are more realistically placed in a specialized subfamily (Paracorophiinae) within family Isaeidae.

Biogeographic and behavioural analysis.

The distribution of genera and species of Corophiinae in the North Pacific region is summarized in Table II, (p. 135). Some 34 species are included, all but one (*C. carlottensis*, n. sp.) previously recorded from the region. Although Otte (1976) included *C. clarencense* (Shoemaker) in his treatment of corophiins of British Columbia, the species had been previously recorded only from the extreme northern Bering Sea and North Greenland (Shoemaker, 1920; Just, 1970), and marginally within the present biogeographical analysis.

The North American Pacific corophiin fauna encompasses 16 species in 5 genera, of which 4 species and 1 genus are almost certainly regionally synanthropic. The Asiatic North Pacific fauna is somewhat more diverse and encompasses 20(21?) species in 6 genera, of which 5 species and 1 genus are considered regionally synanthropic.

The North Pacific corophiinids exhibit very high regional endemicity, amounting to ~75%of the total fauna. Thus, species of four Asiatic-endemic genera (*Eocorophium, Sinocorophium, Microcorophium,* and *Lobatocorophium*) do not occur naturally along North American shores and, in fact, nowhere else. Conversely, the genus *Americorophium* is largely endemic to the Pacific coast of North and Central America\ and sparsely in the tropical and warm-temperate western Atlantic, somewhat resembling that of the *Bemlos* clade of the Aorinae (Myers, 1988). With respect to thermal affinities, primitive burrowing species occur only along warm-temperate and temperate coastlines of both continents; none reaches subarctic or arctic shores. However, a few specialized members of the polymorphic advanced tube-building genus *Monocorophium* (e.g., *M. clarencense, M. crassicorne. M. bonelli,* and *M. steinegeri*) are essentially arctic and arctic-boreal in distribution. More advanced species of *Monocorophium*, and known species of the *Apocorophium* complex, are restricted to temperate and warm-temperate waters.

Synanthropic species encompass almost exclusively colonial tube-builder species of the advanced genera *Monocorophium* and *Apocorophium.* Except for *Sinocorophium alienense,* believed to have become established in San Francisco Bay through shipments of clams and oysters from the Orient (Chapman, 1988), North Pacific burrowing species are otherwise not synanthropic. Similarly, European endemic burrowing species of the genera *Corophium, Medicorophium* and *Chelicorophium* occur nowhere else synanthropically. *Corophium volutator* occurs both in northwestern European waters, and in the Gulf of Maine region of North America, but this distribution is considered naturally amphi-Atlantic (Bousfield, 1973).

Corophiins and Siphonoecetins: compartive biology.

The world distributions of corophiin and siphonoecetin amphipods appear to be mutually exclusive, or nearly so. Thus corophiins are dominant in boreal and temperate regions of the Northern Hemisphere (10 genera vs. only 1 genus of Siphonoecetinae). About 6 species of *Siphonoecetes* overlap with corophiins in the North Atlantic. Corophiins are dominant in the North Pacific along both North American and Asiatic coasts, whereas siphonoecetins, except for a few bubocorophiids in Japan and some concholestids on the Central American coast, are virtually absent. Unlike siphon-

TABLE II. DISTRIBUTION OF GENERA AND SPECIES OF COROPHIINAE IN THE NORTH PACIFIC REGION (* synanthropic record).

GENUS	BIOGEOGRAPHIC ZONE									
	1	1A	2	3	4	5	6	7	8	9
1. *Eocorophium*, n. g.										
E. kitamori (Nagata)	X	X								
2. *Sinocorophium*, n. g.										
S. japonica (Hirayama)		X								
S. sinensis (Zhang)	X	X								
S. lamellatum (Hirayama)	X	X								
S. heteroceratum (Yu)	X									
S. intermedium (Ngoc)	X									
S. homeoceratum (Yu)	X									
S. minutum (Ngoc)	X									
S. orientale (Schellenberg)	X									
S. triangulopedarum (Hir)	X									
S. alienense (Chapman)	?							X*		
3. *Microcorophium*, n. g.										
M. miospinulosum (Hirayama)	X									
4. *Lobatocorophium*, n. g.										
L. lobatum (Hirayama)		X								
5. *Hirayamaia n. g.*										
H. hongkongensis (Hirayama)	X									
H. mortoni (Hirayama)	X									
H. tridentium (Hirayama)	X									
6. *Apocorophium*, n. g.										
A. acutum (Chevreux)		X*								
7. Crassicorophium, n. g.										
C. bonelli (M. E.)			X	X	?					
C. crassicorne (Bruz.)	x?	X	X	X	X	X	X	X		
8. *Monocorophium*, n. g.										
M. steinegeri (Gurjanova)			X	X	X	X	?			
M. carlottensis n. sp.				x	X	X				
M. acherusicum (Costa)	X*	X*	X*		?	X*	X*	X*	X*	
M. insidiosum (Crawford)	x*	X*					X*	X*	x*	X*
M. uenoi (Stephensen)	X	X	x?						X*	X*
M. sextonae (Crawford)		X*								
M. californianum (Shoemaker)							x	X	X	x
M. oaklandensis (Shoemaker)									X	
9. Laticorophium, n. g.										
L. baconi (Shoemaker)	X*			?	X	X	X	X	X	x
10. *Americorophium*, n. g.										
A. brevis (Shoemaker)			?	x	X	X	X	X	X	
A. spinicorne (Stimpson)					X	X	X	X	X	
A. salmonis (Stimpson)						X	X	X		
A. stimpsoni (Shoemaker)							x?	X		

BIOGEOGRAPHIC ZONES: 1. East & South China Seas; **1A.** SE Sea of Japan; **2.** Sea of Okhotsk & NE Sea of Japan; **3.** Bering Sea & Aleutians; **4.** Southeastern Alaska; 5. Northern B. C.; **6.** Southern B. C.; **7.** Wash.-Oregon; **8.** Northern & Central California; **9.** Southern & Baja California. (+ - excl. *H. monospinum* Shen, 1955)

oecetins, a few corophiins *(Crassicorophium* spp.) have penetrated arctic waters.

By contrast in the southern hemisphere, especially in tropical regions, siphonoecetins, particularly concholestids are dominant. Except for a few commercially introduced species, corophiins are rare. However, both groups are rare or lacking in waters around South America and Antarctica.

As noted initially (pp. 70-71), the two groups contrast in behaviour and life style. Thus, all siphonoecetinids are tubicolous. Most are detritivores, but possibly also feed on settling larval stages or meiofauna. The bases of peraeopods 3 & 4 are much broadened and house silk-secreting glands. The silk is used to cement relatively large objects rather than sediment grains to form an abode, or to glue houses of other animals (esp. females) to that of the male. Simple mud tubes are never encountered. The tubes usually have only one entrance. Animals show minimal behavioural response to guard the rear, and no development of the urosome to form a "plug". When feeding currents change, siphonoecetins simply reverse direction of the entire movable house. Peraeopods 5, 6, 7 are similar to those of corophiins in having prehensile hooked dactyls that are adapted to clinging to the inside of the tube.

In sipohoneocetins, antenna 2 is powerful, ambulatory and, paired, used as legs in slow forward crawling, and dragging the isolated moveable abodes, similar to those functions in cerapid ischyrocerids, and many small pagurid decapods. Antenna 2 is also used in a "backwards jumping" behaviour peculiar to many advanced subgroups of siphonoecetins. However, it does not appear to be used in mate guarding or amplexus. Gnathopods 1 & 2 are used in manipulating building materials and/or the abodes of other animals.

In corophiins, only the most advanced members are ful-ly tubicolous. All species are believed to be filter-feeding detritivores but *Microcorophium* may be a micro-carnivore. The bases of peraeopods 3 & 4 are little broadened in strictly burrowing species, but are moderately to strongly so in silk-secreting (abode-building) species. Peraeopods 5 & 6 are short, variously adapted by means of hook spines of segment 5, and by short, curved dactyls that are reversed for clinging to the inside of the tube. However, peraeopod 7 remains elongate and the dactyl ambulatory, not hook-like.

Domicolous corophiids live in fixed abodes, often forming mats of tightly packed tubes, which may be glued to each other. The tubes have two openings. Animals show a strong flipping behaviour within the tube to guard the rear entrance against intruders or to change feeding direction as tidal currents reverse. Advanced species (with fused urosome) block the rear entrance with the modified urosome and uropods. In burrowing corophiins that excavate tubes within the substratum, antenna 2 is equipped with paired apical hook spines and is used in ambulation. However, in males, this appendage apparently functions also in mate guarding and/or amplexus (Conlan, 1991). Primitive corophiins use antenna 2 in burrowing and facilitating first entry into the substratum, and may secondarily line the tube with silk.

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LEGEND FOR FIGURES

A1	**- antenna 1**		**MX2**	**- maxilla 2**	
A2	**- antenna 2**		**MXPD**	**- maxilliped**	
AC FL	**- accessory flag.**		**O. P.**	**- outer plate**	
BR PL	**- brood plate**		**P3-7**	**- peraeopods 3-7**	
CX	**- coxa**		**PL1-3**	**- pleopods 1-3**	
DACT	**- dactyl**		**PLEON**	**- pleon segment**	
DORS	**- dorsal view**		**PLEOS**	**- pleosome**	
EP	**- epimeral plate**		**PLP**	**- palp**	
GN1	**- gnathopod 1**		**RET**	**- retinacula**	
GN2	**- gnathopod 2**		**RT**	**- right**	
HD	**- head**		**SET**	**- seta**	
I. P.	**- inner plate**		**SP**	**- spine**	
LAT	**- lateral view**		**T**	**- telson**	
LFT	**- left**		**U1-3**	**- uropods 1-3**	
LL	**- lower lip**		**UL**	**- upper lip**	
MD	**- mandible**		**UROS**	**- urosome**	
MLR	**- molar**		**VENTR**	**- ventral view**	
MX1	**- maxilla 1**		**X**	**- magnified**	